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Long-Term Dynamics And Silviculture Of Northern Hardwood Forests In The Northeast United States

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LONG-TERM DYNAMICS AND SILVICULTURE OF NORTHERN HARDWOOD FORESTS IN THE NORTHEAST UNITED STATES

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ABSTRACT

Northern hardwood forests are a vast, temperate forest-type existing across much of northeastern North America. In the northeastern U.S., these forests are found from New York to Maine where they have central cultural, ecological, and economic significance. These ecosystems are incredibly variable across this region, growing on a range of sites and influenced by a suite of biotic and abiotic conditions. Developing management regimes that accommodate the ecological complexity of these forests has been the focus of silvicultural studies for decades; however, this work has been constrained by temporal and spatial limitations. As such, there is still uncertainty regarding the evolution and variability of northern hardwood forests over time and across sites under different management scenarios. To address this uncertainty we synthesized long-term silvicultural studies (20 years +) throughout the northeast and assessed outcomes as they related to management objectives and changing forest conditions. Specifically, we explored the regeneration dynamics and development of overstory conditions for even and uneven-aged systems with four distinct approaches. First, we established context for this work through review of existing silvicultural research and analysis of the current northern hardwood resource. Next, we applied long-term, regional inventories to consider abiotic and biotic factors influencing recent sugar maple (*Acer saccharum*) establishment and survival. We then evaluated long-term outcomes of commonly applied even and uneven-age silvicultural systems across a range of sites in New York and New Hampshire using repeated inventories from long-term research trials. Finally, we followed the evolution of gap dynamics over eight decades in the oldest group selection study in North America; research established at the Bartlett Experimental Forest in New Hampshire in the early 1930s. Cumulatively, results showed a frequent disconnect between structure and composition of the overstory and regeneration layers, and the potential for future challenges to sustaining current overstory species. In addition, this work highlighted the pervasive, negative influence of American beech (*Fagus grandifolia*) across the region on regeneration of desired species, namely sugar maple and yellow birch (*Betula alleghenesis*). Outcomes from this work suggest that a variety of silvicultural systems can be used to maintain and regenerate northern hardwood forests; however favorable outcomes require careful consideration of site conditions with management regimes tailored accordingly.

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INTRODUCTION

From Minnesota to New Brunswick, millions of hectares in North American are classified as northern hardwood forest (Burns, 1983; Rowe, 1972). This deciduous and temperate forest-type can be comprised of many species, although it is traditionally defined by a climax composition of shade-tolerant sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) (Braun, 1935; Stearns, 1949). Common associates include birch species, primarily yellow birch (*Betula alleghaniensis*) but also paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), ash (*Fraxinus* spp.) and mixed conifers (*Picea*, *Abies*, and *Tsuga* spp.) (Burns and Honkala, 1990; Westveld, 1956). Composition of a given stand is attributed to a variety of factors, including soil characteristics (Leak, 1978; Seymour, 1994), developmental stages (Oliver and Stephens, 2017; Schwartz et al., 2001), climate (Iverson, L.R., Prasad and Low, 2001), and past land use (Hall et al., 2017; Loo and Ives, 2003). These attributes, as well as processes and dynamics like diseases and insects (Houston, 1975; Lovett, G. M., Weiss, M., Liebhold, A. M., Homes, 2016), browsing by herbivores (Forrester et al., 2014; Nuttle et al., 2013), and level of canopy disturbance (Beaudet et al., 1999; Moore et al., 2008) can strongly influence forest structure and regeneration success on a given site.

Since the early days of northern hardwood silviculture, forest managers and researchers alike have explored even and uneven-aged systems in an effort to maximize productivity and meet increasingly diverse management objectives (Eyre and Zillgitt, 1953; Leak et al., 1987). Yet, consistently capturing the ecological complexity of these forests through management remains a challenge, especially in the face of changing conditions (D'Amato et al., 2011; Spittlehouse and Stewart, 2004). Distinct regional

issues across the range of northern hardwoods also exist, spurring the need for silviculture systems adapted to the site rather than seeking a universal prescription (Fahey et al., 2018; Smith, 1972).

This work focuses on northern hardwood forest of the Northeast United States, considering ongoing silvicultural challenges and opportunities through four separate, but complementary analysis. Chapter 1: *Northern Hardwood Silviculture at a Crossroads: Sustaining a Valuable Resource under Future Change* synthesizes the decades of northern hardwood literature, evaluating the outcomes of different silvicultural systems and their success in meeting defined management objectives. The first chapter additionally quantifies the current northern hardwood resource with data from the U.S. Forest Service Forest Inventory and Analysis program. Chapter 2*: Identifying Factors Affecting Regional Patterns of Sugar Maple Regeneration in Northern New England and New York* takes a further step in exploring abiotic and biotic drivers of regional sugar maple regeneration patterns, using machine learning techniques. Chapter 3: *Long-Term Regeneration Dynamics across a Range of Silvicultural Intensities and Sites in Northern Hardwoods* assesses the outcomes of even and uneven-age treatments from studies in New York and New Hampshire. Specifically, the third chapter explores evolution of advance regeneration over time (20+ years) and changes to forest composition and structure by site and treatment. Chapter 4: *Long-Term Evolution of Composition and Structure after Repeated Group Selection over Eight Decades* analyses results from one of the longest running group selection treatment in North America, located at the Bartlett Experimental Forest in New Hampshire. Findings from the forth chapter contrast development of individual cohorts relative to the broader matrix and consider this

silvicultural approach for maintaining species and structural diversity with time. The final *Conclusions* chapter broadly summarizes emerging themes from this work in terms of scientific findings and management recommendations and highlights weaknesses and potential future directions for research that builds on this dissertation.

CHAPTER 1: NORTHERN HARDWOOD SILVICULTURE AT A CROSSROADS: SUSTAINTING A VALUABLE RESOURCES UNDER FUTURE CHANGE

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1.1. Abstract

Silviculture in northern hardwood forests has been the focus of forestry research in North America for over a century, spanning a wide range of site types, silvicultural approaches, and management objectives. Yet, despite the diversity of this forest ecosystem and demonstrated success under different silvicultural systems, management methods and preference have oscillated in search of a universal approach that is effective at meeting long-term economic and ecological objectives across the range of site conditions characterizing these ecosystems. We synthesize decades of research on northern hardwood silviculture and assess the current status of this valuable forest type. Findings highlight the variability of northern hardwood forests across the northeast and silvicultural challenges to maintaining structural and compositional diversity. The implications of recent and long-term outcomes of northern hardwood silviculture research are considered in the context of meeting traditional and contemporary management objectives, especially in the face of changing forest and environmental conditions.

1.2 Introduction

Northern hardwoods are a broad forest type classification, encompassing an ecologically, economically, and culturally significant ecosystem found across the northeastern U.S. and southeastern Canada. From the Lake States to New Brunswick, the northern hardwood forest covers approximately 20 million hectares (Leak, 1987; Rowe, 1972), primarily classified by presence of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*) together or in association with other hardwood and softwood species (Eyre, 1980; Halliday, 1937, OMNR 1998). Compositional guidelines are one approach to define northern hardwoods, but species mixtures, development, and growth can vary greatly from stand to stand across a given landscape. This variation is often driven by biotic and abiotic factors including land use history (Foster, 1992; Orwig and Abrams, 1994; Schulte et al., 2007), species' ecological requirements (Burns and Honkala, 1990, Tubbs et al. 1983), wildlife dynamics (Horsley and Marquis, 1983; Sage et al., 2003), disturbance regimes (Lorimer and White, 2003), and local site and climate (Barnes et al., 1982; Leak, 1978; Nichols, 1935). Regardless of compositional variation, changing climate conditions and an increasing prevalence of non-native insects, diseases, and plant species have generated great uncertainty regarding the future sustainability of this important forest type.

Existing strategies for managing northern hardwoods are grounded in decades of research, beginning with exploration into approaches for generating a sustained yield; a common guiding paradigm for research in many forest types in the early 20th century. Two USFS Experimental Forests were central to developing early procedures for

achieving this objective, the Dukes Experimental Forest (originally referred to as the Lake States Experimental Forest) in the Upper Peninsula of Michigan and the Bartlett Experimental Forest in the White Mountains of New Hampshire. Foundational studies from each of these locations assessed harvest intensities of different silvicultural systems and subsequent effects on forest composition and structure (Eyre and Zillgitt, 1953; Gilbert and Jensen, 1958). These early works established silvicultural recommendations that continue to be used in many regions today (Arbogast Jr, 1957; Pond et al., 2014). Successive research has investigated species response to habitat (Carmean, 1999; Leak, 1982, 1980), the role of competing vegetation (Nyland et al., 2001; Smith et al., 1988), and how to emulate natural disturbances (Franklin et al., 2007; Seymour et al., 2002) in an effort to create consistent and effective silvicultural systems. But, as forest conditions change so to do management objectives (Butler and Leatherberry, 2004) and preferred silvicultural methods (D'Amato et al., 2017). In addition to goals of sustained yield and forest health, management must also contend with evolving forest threats, such as climate change (D'Amato et al., 2011; Parker et al., 2000; Webster et al., 2018) and an increasing number of invasive species and diseases (Dukes et al., 2009; Waring and O'Hara, 2005). Given the increasingly complex nature of northern hardwood forests and the evolving challenges to management, silvicultural responses require careful evaluation of all available options rather than a single blanket prescription.

Throughout the history of northern hardwood silviculture, use of and preference for different systems has oscillated between extremes, often in the search for a universally applicable approach (O'Hara, 2002; Smith, 1972). Unfortunately, such oscillation may leave valuable tools and management strategies out of consideration

(O'Hara, 2001; Pond et al., 2014). In the context of northern hardwoods, numerous studies have shown successful development of these forests with a wide range of silvicultural systems (Burns, 1983; Leak et al., 2014; C H Tubbs, 1977) and conversely, inconsistent results when the same method is applied across different conditions or locations (Bédard and Majcen, 2003; Neuendorff et al., 2007; Nyland, 1998). In light of ongoing challenges to the long-term sustainability of northern hardwood forests, determining the appropriateness of different silvicultural treatments along the spectrum of even to uneven-age systems is increasingly important. To address this need, we synthesize decades of literature and research on tested silvicultural strategies to provide a broad management context for current and future challenges. Although insights and examples are considered across the range of northern hardwood forests, we focus here on work from the northeastern United States and adjacent Canada. Further, we assess the current status of northern hardwood forests using data from the U.S. Forest Service Forest Inventory and Analysis program and calculated metrics related to forest structure, composition, and regeneration. Implications from the literature review and data analysis are then considered in the context of forest resiliency and adaptation, specifically in the face of changing management objectives and future uncertainty.

1.3 Historic Factors and Natural Conditions

Silvicultural systems for northern hardwood forests have long been governed by compositional and structural goals in conjunction with other carefully applied management strategies (Eyre and Neetzel, 1937; Jensen, 1943; Leak et al., 1969). However, effective management also incorporates the underlying attributes driving the current forest condition. For this work, we consider the ecological needs of key species

that define the northern hardwood forests of the northeast and factors that have shaped their development, specifically natural disturbance regimes (Long, 2009; Nuttle et al., 2013), land-use history (Foster et al., 2008; Hall et al., 2002), and habitat (Leak, 1978; Schwartz et al., 2003).

1.3.1 Silvics and Site Requirements of Northern Hardwood Species

There are many northern hardwood variants, but this temperate, deciduous ecosystem is generally classified by a mature forest where sugar maple is dominant, frequently in association with yellow birch and American beech (Leak et al., 1987; Seymour, 1994). Inclusion of species like red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), white ash (*Fraxinus americana*), or softwoods is driven largely part by site and disturbance history (Eyre et al. 1980; Westveld, 1956).

Soil properties in the northern hardwoods are closely tied to stand productivity as well as species composition (Johnson et al. 1987). Sugar maple, a preferred species for its high economic and social value, increases in abundance on enriched sites with well drained soils (Lindsey et al., 1965; Nyland, 1999). However, the high site requirements for sugar maple often limit the occurrence of pure stands without direct management intervention (Godman et al. 1990). Yellow birch, also an economically desirable and ecologically important tree, has lower site requirements than sugar maple and correspondingly can occur across a wider range of suitable locations (Erdmann 1990). Where underlying soils are derived from fine to sandy tills and canopy disturbances include large gap and mesoscale events, yellow birch can be a significant component of northern hardwood forests in later developmental stages (Godman and Krefting, 1960; Leak, 1980). American beech can grow on a range of sites as well, including those with

lower pH and poorer drainage (Tubbs and Houston 1990). Beech is especially suited to low light levels (Canham et al., 2016) and often becomes the dominant species without canopy disturbance on fine and sandy till soils (Leak, 1978; Nyland, 1999). This natural successional trajectory is reflected in early land survey records in the northeastern United States in which American beech was the dominant canopy species across many areas now supporting northern hardwood forests (Thompson et al., 2013). The abundance of important, minor species like red maple, eastern hemlock (*Tsuga canadensis*), white ash, and American basswood (*Tilia americana*) is also controlled by their silvics and required soil properties. Red maple can be found on sites with poor drainage, even periods of standing water (Johnson 1987), while eastern hemlock importance decreases in northern hardwood forests with increasing soil drainage (Woods, 2000). Both ash and basswood increase in composition on sites with higher levels of nutrients (Burns and Honkala, 1990). Collectively, soil fertility and drainage have been recognized as key controls on the establishment and productivity of northern hardwoods and have been an integral part of guidance for selecting appropriate silvicultural systems over the past half century (Leak, 1982, 1980, 1978).

Similar to the importance of soil properties, successional dynamics and light availability also drive composition in the northern hardwood ecosystem. Sugar maple and beech are highly shade tolerant species that can persist under low light conditions for decades (Canham, 2010), while yellow birch is considered mid-tolerant, and intolerant species like paper birch or white ash decrease in dominance as the forest ages if moderate to heavy levels of canopy disturbance do not occur (Archambault et al., 1998; Burns and Honkala, 1990; C H Tubbs, 1977). Although level of shade tolerance influences

competition and growth dynamics at each stage of forest development (Holmes and Reed, 1991), this trait may be most important for regeneration response of individual species. Following disturbance, regeneration establishment strategies are closely linked to shade tolerance (See "Natural Disturbance Regimes" section below, Oliver and Larson 1990).

1.3.2 Natural Disturbance Regimes

Scale and severity of disturbance are central drivers of northern hardwood forest development (Oliver, 1981) and emulating these processes was an early basis for ecological forestry (Spurr and Cline, 1942). In the northeast United States, research and observation have long indicated that small-scale events like ice and wind storms are the primary disturbance agents lending to gap-based silvicultural approaches (Lorimer, 1989; Lorimer and White, 2003). However, stand replacing and mesoscale events also drive important aspects of forest development and silvicultural strategies (Bergeron and Harvey, 1997; Seymour et al., 2002). Across the scale of disturbance, return intervals and area disturbed are key characteristics. In the northeast, small scale disturbances, those that create natural canopy gaps, occur every 50-200 years establishing patches between 4 and 1135 m^2 while larger stand replacing events, primarily wind and fire, occur every 800 to 9,000 years disrupting 1 to >80,000 ha (Seymour et al., 2002). The scale and frequency of mesoscale disturbances, like wind and insect outbreaks, are intermediate relative to small and large-scale events, playing an equally important role in the dynamics of northern hardwoods (Jenkins, 1995; Wood et al., 2009).

Scale of disturbance is especially influential to composition as species exhibit differences in physiological and morphological responses along a gradient of light

availability (Beaudet and Messier, 1998; Gasser et al., 2010) Smaller events favor more shade tolerant species and advance regeneration (Digregorio et al., 1999; Frelich and Lorimer, 2011). In the northern hardwoods, sugar maple and American beech respond well to these low light conditions (Canham, 2010; Canham et al., 2016). Traditional silviculture systems, primarily single-tree selection and group selection, are most closely aligned with lower intensity natural disturbances (Gasser et al., 2010; Ilisson and Chen, 2009). Increasing canopy disturbance, as seen in meso and large scale events, increases composition of mid and intolerant species important for maintaining species diversity across the landscape (Hanson and Lorimer, 2007; Hill et al., 2005; Lorimer, 1989). In the absence of larger disturbances ,ecologically and economically important species, including paper and yellow birch and white ash, decrease in stands and the broader landscape (Raymond et al., 2006; Shields et al., 2007). Silvicultural systems with larger canopy openings, like group and patch selection, aim to capture these compositional dynamics and may simultaneously align with cohort structures and compositional conditions typically found in old-growth forests (Leak, 1999; Nuttle et al., 2013; Shields et al., 2007). Use of clearcuts and other more intensive management lends to forests initially dominated by intolerant and mid-tolerant species, such as pin cherry, aspen species, paper birch, yellow birch, and white ash where establishment relies on high numbers and fast growth (Marquis and Bjorkbom, 1964; Webster and Lorimer, 2005). Capturing these intricacies of species development and manipulation of species composition has been at the forefront of silvicultural research since the early 1900s (Eyre and Neetzel, 1937; Eyre and Zillgitt, 1953) and continues as a conversation in forest management today (North and Keeton, 2008; Reuling et al., 2019).

1.3.3 Land-Use History and Forest Ownership

The arrival of European settlers to northeastern North America in the early 1600s began the centuries long transition of forests in the region and perhaps had the greatest influences on today's hardwood landscape (Ellis, 2011; Foster et al., 2003; Ramankutty et al., 2010). Land clearing, first for settlements and construction then agriculture and timber, shifted the age and compositional dynamics of forests that had been largely untouched (Cogbill et al., 2002; Hermy and Verheyen, 2007). Existing compositional zones between northern and southern New England led to increasingly divergent forests. Gentler topography and better accessibility led to clearing for agriculture across southern New England and much of the eastern United States during the 18th and 19th centuries (Foster, 1992; Seymour, 1994; Smith et al., 1993). Regions to the north remained largely untouched until late 19th and early 20th century when heavy partial harvesting of spruce and fir for the growing paper industry shifted composition towards hardwoods (Bryant, 1917; Linn, 1918; Westveld, 1949). Through the 1950s, high quality sawlogs were selectively removed from pure hardwood stands leaving behind unmerchantable trees of poor quality and vigor (Blum and Filip, 1963; Hall et al., 2002). This historic land use has resulted in large areas of even-aged northern hardwoods in regions recovering from agricultural abandonment in the late 19th and early 20th centuries and irregular, often degraded stand conditions in other regions where selective logging prevailed (Kenefic and Nyland, 2006).

Ownership patterns continue to drive present day northern hardwood forests. In the northeast United States, forests are primarily owned by private individuals and families where timber extraction is a secondary objective (Leak et al., 2014; Rickenbach

and Kittredge, 2009). Rather, these small land owners manage their woodlands for wildlife habitat and esthetics, cutting trees primarily to offset costs of retaining the property (Kelty et al., 2003). Landowner objectives and concerns subsequently drive silvicultural systems, often aligning better with less intensive management regimes (Emery and Zasada, 2001; Kelty et al., 2003).

1.4 Present Day Challenges and Concerns

Like many other forest systems around the globe, there are several current and emerging stressors and disturbances that have generated great uncertainty and unexpected outcomes as it relates to the long-term stewardship of this resource. Many novel factors, such as atmospheric deposition, affect the current structure and functioning of northern hardwood forests, but for this review we will focus on three primary sources of change: 1) beech bark disease, 2) browsing by herbivores, and 3) changing climate.

1.4.1 Beech Bark Disease

The arrival of beech bark disease at the turn of the last century irreversibly changed northern hardwood forests in eastern North America. This disease complex, which targets American beech, is comprised of the scale insect *Cryptococococcus fagisuga* and fungus *Nectria coccinea* var. *faginata* (Shigo, 1972). Although Beech bark disease (BBD) is native to Europe, it arrived in the U.S. via Nova Scotia in the early 1920s (Houston, 1975). To date, three stages of BBD are recognized, the advancing front, killing front, and aftermath zone (Houston, 1994). The advancing front represents the earliest stages of the disease complex with the scale insect visible on infected trees, but with limited presence of the fungus. The killing front is associated with widespread mortality of beech, particularly on large diameter trees, whereas the aftermath zone is

represented by areas where most large diameter beech have been killed and stands are dominated by smaller, root-sprout origin beech (Houston, 1994, 1975). Over a century after first introduction, much of northeastern North America is in the aftermath zone with few resistant beech remaining and mature trees replaced by dense thickets of root suckers (Giencke et al., 2014; Twery and Patterson, 1983).

Beech has always been a major component of northern hardwood forests in the northeast (Cogbill et al., 2002), but BBD has altered the competitive dynamics between this species and other deciduous trees (Morin et al., 2007; Twery and Patterson, 1983). The shade tolerant nature of beech and the ability to prolifically sucker following harvest or injury complicates management of hardwood forests, especially in systems where sugar maple and yellow birch are preferred (Tubbs and Houston 1990; Jones and Raynal, 1988). In the timing of application of silvicultural treatments, there is often a narrow window where other species can outcompete beech without heavy intervention. In the Adirondack region of New York, Bohn and Nyland (2003) found stands with initially low or very high levels of beech changed little after cutting, however, stands with medium to high levels prior to harvest ran the greatest risk of increasing beech composition to critical levels. Where acceptable, herbicide application has been used to control beech suckering (Kelty and Nyland, 1981; Ostrofsky and Mccormack, 1986), as have harvesting efforts that minimize root damage (Ostrofsky and Houston 1988). However, control of beech composition continues to be an ongoing challenge, specifically with regard to regenerating desirable hardwood species.

1.4.2 Browsing by Herbivores

Competitive interactions between American beech and more economically desired species such as sugar maple and yellow birch are further exacerbated by heavy browse pressure from white-tailed deer (*Odocoileus virginianus*). Relative to maple and birch species, beech is much less palatable to deer and only exposed to light browsing (Tierson et al., 1966). Sage et al. (2003) found establishment of desired hardwood regeneration was controlled largely by three components; the forest light regime, interaction with competing species, and browsing by white-tailed deer. Similar results were observed in West Virginia where high deer populations, 11.5 to 18 deer/km^2, negated the positive influence of light availability from large gaps on species diversity (Nuttle et al., 2013). Yet, while numerous studies demonstrate the influence of deer browse on forest structure and composition, managing for deer populations can be difficult. Historic harvest and climate data from New York indicated local deer populations varied by a series of factors, including winter severity, hunting policies, and ranges of matriarchal groups (Nesslage et al., 2001; Sage et al., 2003). Further, deer management is a topic of interest to a wide range of stakeholders whose objectives do not always align (Woolf and Roseberry, 1998). As such, implementation of silvicultural systems in the northern hardwood forests must be adaptable to high levels of herbivory.

1.4.3 Climate Change

Globally, forests store approximately 45% of terrestrial carbon, and as such have been highlighted as a critical component of climate change mitigation strategies (Bonan, 2008). Yet, as climate conditions change, uncertainty exists about the future frequency of

forest disturbances, shifts in resource availability, and ultimately movement of species ranges (Dale et al. 2001; Iverson et al. 2001; Sykes et al. 2016). Additionally, the influence of invasive species and diseases is anticipated to increase under climate change scenarios (Lovett, et al. 2016). Specifics for the direct impacts of climate change are difficult to predict with certainty, but field observations and model scenarios offer some insight. A very likely outcome is loss of species richness as species' ranges shift with changing climate conditions; an expected dynamic in the birch-aspen and maple-beech-birch forest types that comprise the northern hardwoods (Janowiack et al. 2017; Scheller and Mladenoff, 2005; Iverson et al. 2001). For sugar maple in particular, changing climate will likely trigger severe stress and decline outside zones of climate refugia (Oswald et al., 2018). Shifting ranges of invasive diseases and insects are also likely to have negative impacts are hardwood forests, although determining specific dynamics is complicated (Hellmann et al., 2008). Beech bark disease and forest tent caterpillar (*Malacosoma disstria*), a native defoliator, are two important disturbance agents in northern hardwood forests that may benefit from warmer climates, especially during winter months (Dukes et al., 2009). The intensity and frequency of natural disturbances are also anticipated to increase with climate regimes including droughts (Dale et al., 2001), windstorms (Peterson, 2000), and ice storms (Rhoads et al., 2002 ; Irland 2000).

Managing forests for adaptability and resiliency has been suggested as an approach that may allow forests and forest managers to buffer the uncertainty of future conditions (Spittlehouse and Stewart 2003, Millar et al. 2016). Analysis of the outcomes of long-term silviculture studies in the Great Lakes region of the United States found multi-aged approaches such as single-tree selection or irregular shelterwood may be the

most effective at balancing mitigation and adaptation at the stand level (D'Amato et al. 2011). A key aim of work examining the tradeoffs between the mitigation and adaptation is examining outcomes of silvicultural systems in the context of the future functional response of a given forest, as opposed to a strictly species-centered focus (Curzon et al., 2017; Olson et al., 2017; Puettmann 2009).

1.5 Silvicultural Systems and Other Management Responses

Silvicultural systems across northern hardwood forests in northeastern North America have long sought to maximize forest production through preferred species mixtures and sustainable yield. Increasingly, forest management also looks for silvicultural solutions to more contemporary challenges like maintaining native biodiversity or increasing resilience to a changing climate or unpredictable market conditions. As such, preference for silvicultural systems fluctuates between extremes of even and uneven-age approaches over time (Smith, 1972).

1.5.1 Even-age Systems

Even-age forests, although naturally occurring in the northern hardwoods, are more frequently the product of historic, intensive land-use or more recent harvesting history. Clearcutting and uniform shelterwood systems have been applied in the region since the early period of formalized forest management to create even-age conditions (Leffelman and Hawley 1925); however, these approaches have not experienced the wide-spread popularity of uneven-age silvicultural systems such as group and single-tree selection. In part, the limited application of even-age silviculture at a broad scale is due to historic and ongoing public reaction to these silvicultural systems relative to other, less intensive approaches (Hannah, 1988; Kelty et al., 2003). This is especially true of

clearcutting. Public opposition to clearcutting is wide spread with many Americans associating the practice with environmental decline and inferior management (Bliss, 2000). In some instances, public responses to clearcutting have initiated policy debates and reform in an effort to regulate use on federal (Fairfax and Achterman, 1977; Spurr, 1981) and private lands (Steelman and Ascher, 1997). Yet, despite constraints to these approaches, clearcutting has been demonstrated as an economical and efficient method for managing northern hardwoods, favoring more shade intolerant species (Hornbeck et al., 1986; Metzger and Schultz, 1984). In central New York, clearcutting increased species diversity in the regeneration layer (Wang and Nyland 1993) and resulted in stands with high stocking of commercially valuable species including sugar maple and yellow birch (Walters et al. 1989). Complete removal of the overstory in clearcuts also creates needed habitat for early successional bird species (Costello et al., 2000; Yamasaki et al., 2014) as well as mammals, reptiles, and amphibians that rely on young forest conditions (DeGraaf and Yamasaki, 2003). Although benefits of clearcutting are clear, ecological concerns exists as well, especially reduction in biodiversity of non-tree species and loss of mature forest legacies critical to sustaining certain species and processes in regenerating forests (Rudolphi et al., 2014). Increasing mature tree retention, specifically large biological legacies, is an increasingly common strategy to address these concerns (Gustafsson et al., 2010).

Shelterwood systems offer another even-age approach where public opinion or policy guidelines make widespread implementation difficult (Hannah, 1988). Outcomes may vary by the number of entries, time of harvesting, and density of the overwood, but when these attributes are appropriately matched to stand conditions and objectives,

shelterwood cutting is an effective method for regenerating northern hardwood forests (Godman and Tubbs, 1973; Hannah 1991). Research from the Adirondack region of New York showed ample regeneration of yellow birch, sugar maple, and white ash in deer exclosures following a two-stage shelterwood; outside exclosures, regeneration was dominated by beech and hobblebush (Curtis and Rushmore, 1958). Kelty and Nyland (1981) saw similarly abundant regeneration of desirable species using a two-stage shelterwood in combination with hunting to reduce populations of white-tailed deer and pretreatment mist blowing of herbicides to remove advance regeneration of beech. A crucial component of shelterwood systems is layout of the final harvest to remove the overwood. Jacobs (1974) observed 35% of regeneration was damaged during the removal cut in a northern hardwood stand, but overall reproduction was successful due to large numbers of regeneration following the initial cut. Yet, economic and operational difficulties in removing the overwood (Leak et al., 2014) and landowner preference for less intensive management (Kelty et al., 2003) remain reasons uniform shelterwood systems have not been more widely adopted in northern hardwood forests of the northeast.

An alternative approach to uniform shelterwood systems is the irregular shelterwood system. Primarily in eastern Canada, but also in New England (Peterson and Maguire, 2004), irregular shelterwoods have been proposed as a hybrid of traditional even and uneven-aged management for mixedwood and hardwood forests (Raymond et al., 2009). Irregular shelterwood systems are an approach to capture the ecological complexity, particularly species composition and structure, of forests following mesoscale disturbances (Raymond and Bédard, 2017). The continuous cover and

expanding gap versions of this system have increased spatial and temporal flexibility relative to traditional shelterwood, single-tree, and group selection methods to meet these objectives (Raymond et al., 2009). In Quebec, Canada continuous cover and extended irregular shelterwood systems have been employed to rehabilitate impoverished northern hardwood stands following repeated selective cutting (Bédard et al., 2014). For stands with a low percentage of acceptable growing stock and high component of American beech, Bédard et al. (2014) found irregular shelterwood systems may be more appropriate than single-tree selection if desired species are those that could be regenerated in groups; however, cutting cycle lengths would need to be greater than those used in single-tree selection given heavier volume removals at each entry. Initial results for irregular shelterwood studies are promising in terms of increasing species and structural diversity, metrics of increasing importance when assessing forests for changing climate and market conditions (Kern et al., 2017).

1.5.2 Uneven-age Systems

Early research on northern hardwood silviculture emphasized growth and yield following a period of heavy selective harvesting (Hawes and Chandler 1914; Eyre and Neetzel 1937; Hough and Taylor 1946). From this research, preliminary guidelines were developed for single-tree selection based on theoretical balanced stand conditions aimed at sustaining a regular supply of forest products over time and improving growth of the residual stand (Eyre and Zillgitt, 1953). Long-term research across the range of northern hardwoods has demonstrated successful regeneration and increased stand quality with careful application of single-tree selection, especially with efforts for beech control and

deer browse impacts (Jones et al., 1989). The implementation of single-tree selection has been most appropriate on sites where an increased abundance of tolerant species that yield high value products are desired results (Keyser and Loftis, 2013; Leak et al., 1987). Efforts to regenerate and maintain mid-tolerant species after repeated applications of single-tree selection have not been as successful (Johnson 1984; Neuendorff et al. 2007; Lorimer 1989). Further, the challenge of creating and maintaining a truly balanced stand structure (Hicks, 1998), and the high skill level of staff required for implementation (Brockway et al., 2015) have increased the interest in alternative options for northern hardwood management.

Group and patch selection are additional strategies for northern hardwood management, noted for maintaining uneven-age structure while recruiting mid-tolerant and tolerant species (Leak, 1999; Poznanovic et al., 2013). Long-term data from New England demonstrated that increased light in group selection relative to single-tree selection increased the component of desirable species, namely yellow birch and sugar maple, by providing a competitive advantage over beech (Leak and Filip, 1977; Leak, 1999). This approach may also offer productivity benefits, as a study of northern hardwoods in Wisconsin showed increased growth in small group openings relative to single-tree selection openings with productivity reaching an asymptote as gaps size increased above $100m^2$ (Webster and Lorimer, 2005). While still considering structure of the stand, group selection offers increased flexibility in target diameter distributions where marking is driven by presence of advance regeneration or pockets of economically mature trees (Leak and Gottsacker, 1985). Patch selection is similar to group selection and regarded as an additional method for increasing composition of mid and tolerant

species by creating larger openings, between 0.1 to 0.8 ha in size, using within-stand area regulation, while removing single trees throughout the surrounding matrix (Leak et al. 2014; Nyalnd 2015). Where a persistent beech understory is present, harvest operations can serve a twofold purpose by removing beech advance regeneration and creating an early competitive advantage for more desirable species (Leak, 2005). The greater opening sizes in patch selection have added wildlife life benefits increasing early seral habitat (Yamasaki et al., 2014).

Group and patch selection have become increasingly popular methods for managing northern hardwood forests, but as seen in other common silviculture systems, are not without their limitations. An especially critical component to group and patch selection is layout of openings. Arbitrary application of openings in a uniform to semi-uniform fashion disregard the benefits of these treatments for accommodating spatial variability in stands through removing patches of mature overstory trees or releasing areas stocked with desirable advance regeneration (Murphy et al., 1993; Minckler 1986). Considering appropriate orientation and shape of openings is also necessary to ensure consistent results (Marquis, 1965). Over time, group and patch selection can increase the complexity of the forest by diversifying age structures and composition, which may have ecological benefits (Hanson et al., 2012), but the mosaic of even-aged groups created by this approach may complicate long-term management actions (Murphy et al., 1993).

1.6 The Current Status of Northern Hardwoods

Before considering future management actions and implications for the northern hardwoods we assessed the current status of this resource across the northeastern United States. Our assessment utilized regional forest inventory data from the U.S. Forest

Service Forest Inventory Analysis program (https://fia.fs.fed.us). The Forest Inventory Analysis program (FIA) is a national census comprised of a network of permanent sample plots established on a grid system across the United States. The inventory plot is constructed of four, circular 7.2 m radius subplots with nested micro-plots using a radius of 2 m. All trees ≥ 12.7 cm DBH are measured on subplots, while saplings (2.5 to 12.4 cm DBH) and seedlings (< 2.5 cm DBH, height ≥ 15.2 cm for softwood species, ≥ 30.4 cm for hardwood species) are measured on micro-plots. Plots are re-measured on an approximately 5-year cycle (USDA 2007). For this work FIA data were selected from the most recent and complete inventory of each state.

1.6.1 Study Area

The study area for this analysis is northern hardwood forests of Maine, New Hampshire, Vermont, and New York. Plots included were those classified as northern hardwoods by FIA using forest type code 801 (Burrill et al., 2018) (Figure 1-1). The region is humid and cool, with average annual precipitation between 80 to 130 cm and range in elevation from 150 to 460 m. Soils throughout the study area can be quite variable, but are generally classified as podzols (Seymour 1995; Lull 1968). Analysis was completed using R statistical software (https://www.r-project.org/).

1.6.2 Data Analysis

To assess the northern hardwood resource in New England and New York we considered overstory and regeneration characteristics that were directly measured by FIA field crews or easily calculated from published FIA data. For the overstory species, importance values (IV) were used to compare differences in composition between states,

while quadratic mean diameter (QMD), approximate stand age, density (trees ha^{-1}) and basal area (m^2ha^{-1}) evaluated overstory structure. QMD was included as an alternative measure of stage of stand structural development appropriate in forests that may have multiple age classes (Lorimer and Frelich, 1998).

Importance values were also determined for regeneration size classes in each state as well as stocking (%) and density (trees ha^{-1}). Due to the variable nature of seedlings and seedling data, only advance regeneration (trees 2.5 to 12.4 cm DBH) was used for this analysis.

Species importance values were determined using the following formula:

$$IV = (RDen + RDom)/2$$

Where RDen is the relative density of a single species measured in trees per hectare and RDom is the relative dominance of a species measured by basal area in $m^2\,ha^{-1}$. To capture general species trends, data were divided into the following species groups: American beech, sugar maple, yellow birch, other hardwoods, and softwood species.

QMD was calculated as a function of basal area following methods outlined by Curtis and Marshall (2000). Approximate age was derived from the FIA variable STDAGE where age is determined in the field during annual inventories (Burrill et al., 2018). Results for QMD, approximate age, density, and basal area were presented using box plots by state.

Average stocking of regeneration (%) by state was calculated as the number of plots with at least one stem of the following species groups, American beech, sugar maple and yellow birch (desired regeneration), other hardwoods, and softwoods.

Average density and standard error of the same species groups were calculated as trees ha^{-1}.

1.6.3 Current Condition of Northern Hardwood Resources

Overstory composition and ensuing IVs of key species varied by state (Figure 1-2). Sugar maple was most important in Vermont followed by New York, likely reflecting the greater relative abundance of nutrient-rich parent materials in these states relative to New Hampshire and Maine (Leak, 1982). IV values for yellow birch were highest in New Hampshire and Vermont. Beech importance in the overstory was comparable to other desirable species, with the greatest IV in Vermont. Softwood species were also important for all states with the largest value occurring in Maine. Although sites were classified by FIA as northern hardwoods, the IV of softwoods in Maine reflects the greater prevalence of mixed-wood forests in this state (Seymour 1989).

The structural conditions of the overstory exhibited some patterns between states, but primarily highlighted variability for northern hardwood attributes across the region and within states (Figure 1-3). Although not significantly different from other states, QMD, approximate stand age, and basal area were lower in Maine. Distinctions in stand structure between Maine and other states likely reflects the greater proportion of industrial ownerships in this state and long-term history of intensive harvesting in many of these forests (Butler et al. 2014). Additionally, difference in structure between states may be from difference in productivity and site quality across the region (Seymour, 1994).

In the advance regeneration layer sugar maple importance was again highest in Vermont followed by New York while yellow birch IV was comparable across states (Figure 1-4). Higher regeneration numbers for sugar maple again reflect the higher site quality in these states and better competitive ability of sugar maple on these sites. Beech importance; however, increased in each state relative to overstory IVs and exceed importance of desired regeneration (Figure 1-2 and Figure 1-4).

Without consideration of individual species or species groups, all states were well stocked exceeding 75% (Figure 1-5). Total density of advance regeneration also indicated a high level of stocking with states at or above 1000 stems ha^{-1} (Figure 1-6). These values met or surpassed regional regeneration guideless for northern hardwood forests (Leak, 1987; Tubbs, 1977; OMNR). However, when values for individual species were reviewed potential issues with beech regeneration relative to sugar maple and yellow birch were clear. Beech stocking was at or above 20% for all states, lowest in Maine and highest in Vermont, while combined stocking of sugar maple and yellow birch was lower than beech in all states excluding Maine (Figure 1-5). Density of sugar maple and yellow birch was also lower than beech for all states except Maine where values were comparable (Figure 1-6). The increasing and highly competitive nature of beech regeneration has been reported in other regional studies (Bose et al., 2017a; Hane, 2005) and is frequently cited as a barrier to regeneration of more desirable species (Beaudet et al., 1999; Bohn and Nyland, 2003; Nyland et al., 2006). Regional analysis from this work supports these findings and emphasizes the need for thoughtful silviculture to secure healthy and diverse northern hardwood forests into the future.

1.7 Ongoing Work and Recommendations

Long-term silvicultural studies and regional data assessments highlight the unique and variable nature of northern hardwood forests. Further, these assessments show clear challenges for sustaining northern hardwoods in perpetuity, particularly in relation to incongruity between silvicultural outcomes in the forest overstory and regeneration layers. Maintaining a spectrum of silvicultural options across the hardwood landscape provides the best path forward, especially under uncertain climate and forest conditions (Price et al., 2001; Spittlehouse and Stewart, 2004).

1.7.1 Silviculture for Traditional and Evolving Objectives

Traditional management objectives, including compositional and structural targets, continue to be the backbone of northern hardwood silviculture (Leak et al., 2014). Originally, these targets were used to secure sustained yields of commercially valuable species across the landscape for the Northeast's prosperous forest products industry. In recent decades, models of forest industry have changed but maintaining a continuous wood supply remains essential to local economies in the region (EDAT, 2017; Vermont 2013). Increasingly, management guidelines intended for traditional forest products are being reframed to meet contemporary forest objectives like maintaining and restoring native biodiversity (Bolton and D'Amato, 2011; Mitchell et al., 2006) and increasing resilience to climate change (Millar et al. 2007; Nagel et al., 2017). Silviculture for contemporary objectives must grapple with compounding and previously unseen challenges including movement of disease and insects beyond current ranges (Crowl et al., 2008), shifting ranges for dominant tree species (Wilson et al., 2005), and larger,

more intense disturbance regimes (Dale et al., 2001). The spectrum of changes anticipated for northern hardwood forests is wide and the magnitude of impact uncertain. To withstand these imminent transformations applying existing management tools with appropriate modification to increase diversity of species and structure can offer a path forward (Bolte et al., 2009; D'Amato et al., 2011; Keenan, 2015).

1.7.2 Preferred Silvicultural Methods in a Time of Uncertainty

Goals may be clear for traditional and contemporary objectives, such as maintaining sustained yield and increasing diversity, but identifying the silvicultural methods that best achieve these results remains elusive. Ultimately, long-term studies and decades of observations suggest one ideal silvicultural treatment or even an ideal age structure does not exist for northern hardwood forests. Rather, a range of silvicultural methods are appropriate and necessary across the landscape (Nagel et al., 2017; Puettmann, 2011).

Adjusting management approaches to evolving objectives is not new in hardwood silviculture, but creating silvicultural strategies for conditions with no analog is (Puettmann, 2011). For example, non-native and invasive earthworms have no historic context in northern hardwoods, but the decline they trigger in forest health by depleting leaf litter and soil nutrients and reducing sugar maple regeneration opportunities has left forestry practitioners seeking management solutions (Burtelow et al., 1998; Callaham et al., 2006; Lawrence et al., 2003). Where no prior framework exists, forest managers and researchers must return to the fundamentals.

One such principle is matching species with appropriate habitat and careful consideration of existing site conditions (Leak, 1980). This point is well exemplified by management for sugar maple. Sugar maple has long been regarded as a species effectively maintained with single tree selection (Leak, 1982; Nyland, 1999), yet, growth and development under this system fails when treatment is combined with a series of compounding factors including elevated deer populations (Nesslage et al., 2001; Sage et al., 2003), lower site quality (Jones et al., 1989; Leak, 1996), and competition with beech (Bohn et al., 2011). Preserving sugar maple across the northern hardwoods has implications for traditional forest products and maple syrup production, but also ecological conditions like wildlife habitat (Ford 2002) and nitrogen cycling (Lovett and Mitchell, 2004). Most importantly, loss of any species, especially one as abundant as sugar maple has wide reaching implication for ecosystem health and function (Haas et al., 2011; Tilman et al., 1997). Failing to account for influential factors thus becomes increasingly reckless for species such as sugar maple that are anticipated to struggle under changing climate (Iverson and Prasad, 2001).

In instances where site and silviculture can preserve a species, efforts should be done to do so, but management must be equipped for transition of species too. Climate change impacts to species composition and forest processes depend on the severity of change with model predictions under varying future emission scenarios offering some guidance (Dale et al., 2001; Dukes et al., 2009; Iverson, L.R., Prasad and Low, 2001). Encouraging species diversity remains the best approach, but facilitation of new species suited for changing site conditions is a viable approach. For ash species (*Fraxinus* spp.) climate change comes as twofold threat with the introduced emerald ash borer (*Agrilus*

planipennis) (DeSantis et al., 2013). Maintaining the current condition of ash forests seems unlikely, but planting of species with similar ecological roles and cultural attributes may preserve ecosystem function (Iverson et al., 2016; Looney et al., 2017). Successful facilitation and management for resilience requires consideration of many complex and interacting site level attributes, a principle central to sound silviculture, but increasingly more important under changing climate conditions.

Flexibility in management is also central to development of healthy and well-functioning forests under future uncertainty (Dukes et al., 2009; Heller and Zavaleta, 2009). History in the northern hardwoods and other forest types reveals periods of preferences for one extreme of silvicultural options or another (O'Hara, 2002; Smith, 1972). Such actions were restrictive then and would be even more detrimental today. Rather forestry practitioners need to consider all options with the ability to reverse decisions and choose management approaches best suited to their specific objectives and forest conditions (VPR 2015; Millar and Stephens, 2007). In the context of changing future conditions, an overriding objective for selection and application of any given approach should be the maintenance of a wide range of structural and functional conditions at the stand and landscape-level as a precautionary strategy for addressing the uncertainties associated with global change impacts (D'Amato et al. 2011).

1.8 Conclusions

Management of northern hardwood forests in the northeast United States has long interacted with the ecological complexity of these forests and the wide range in desired outcomes. Over time, a range of silvicultural approaches have been used to meet objectives including sustained yield, species compositional goals, and resilience to

climate change. Across objectives, many silvicultural systems have been successfully employed. However, compounding factors, especially site characteristics, make use of a single system or age structure inappropriate. Regional analysis of the northern hardwood resources in New England and New York further revealed the many versions and variability of this important forest. Moving forward into an imminent period of change, silviculture and management must embrace complexity through treatments closely connected to site attributes and flexibility to meet new conditions.

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Figures

Figure 1-1. Map of northern hardwood forest FIA plots

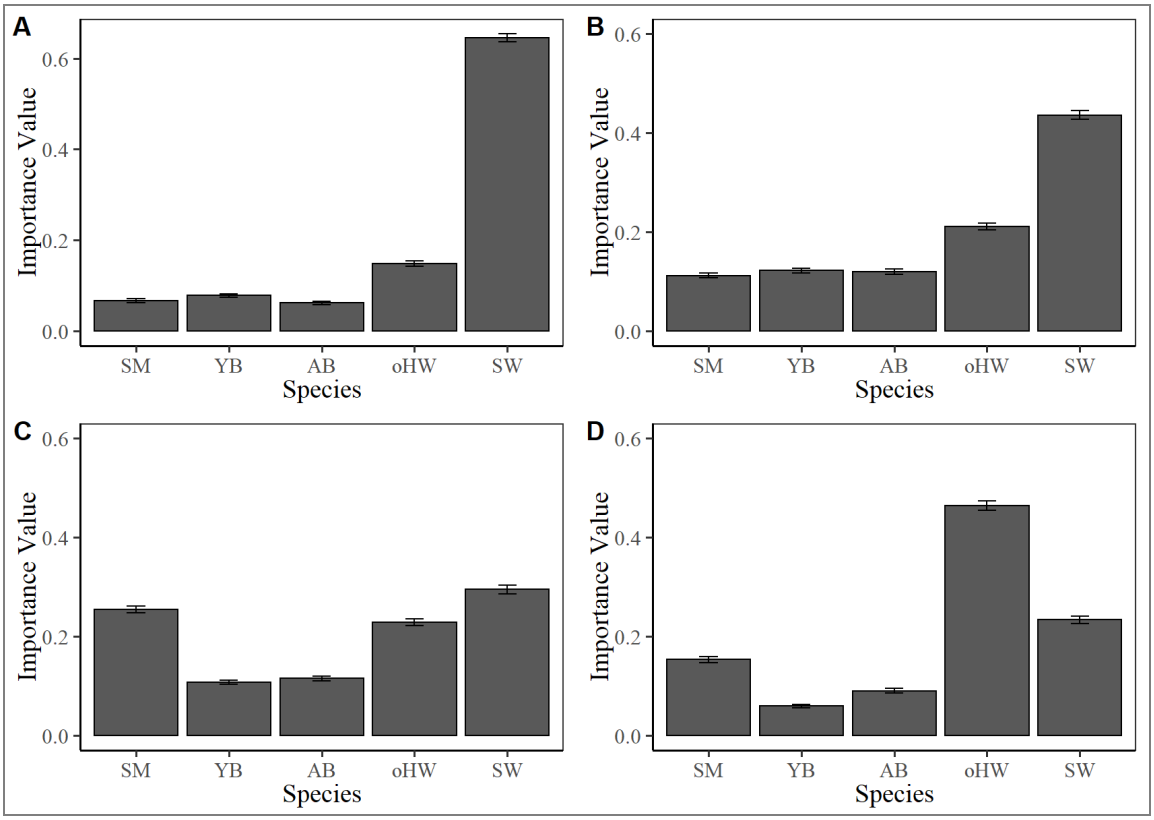

Figure 1-2. Overstory species importance values by state, A: Maine, B: New Hampshire, C: Vermont, D: New York.

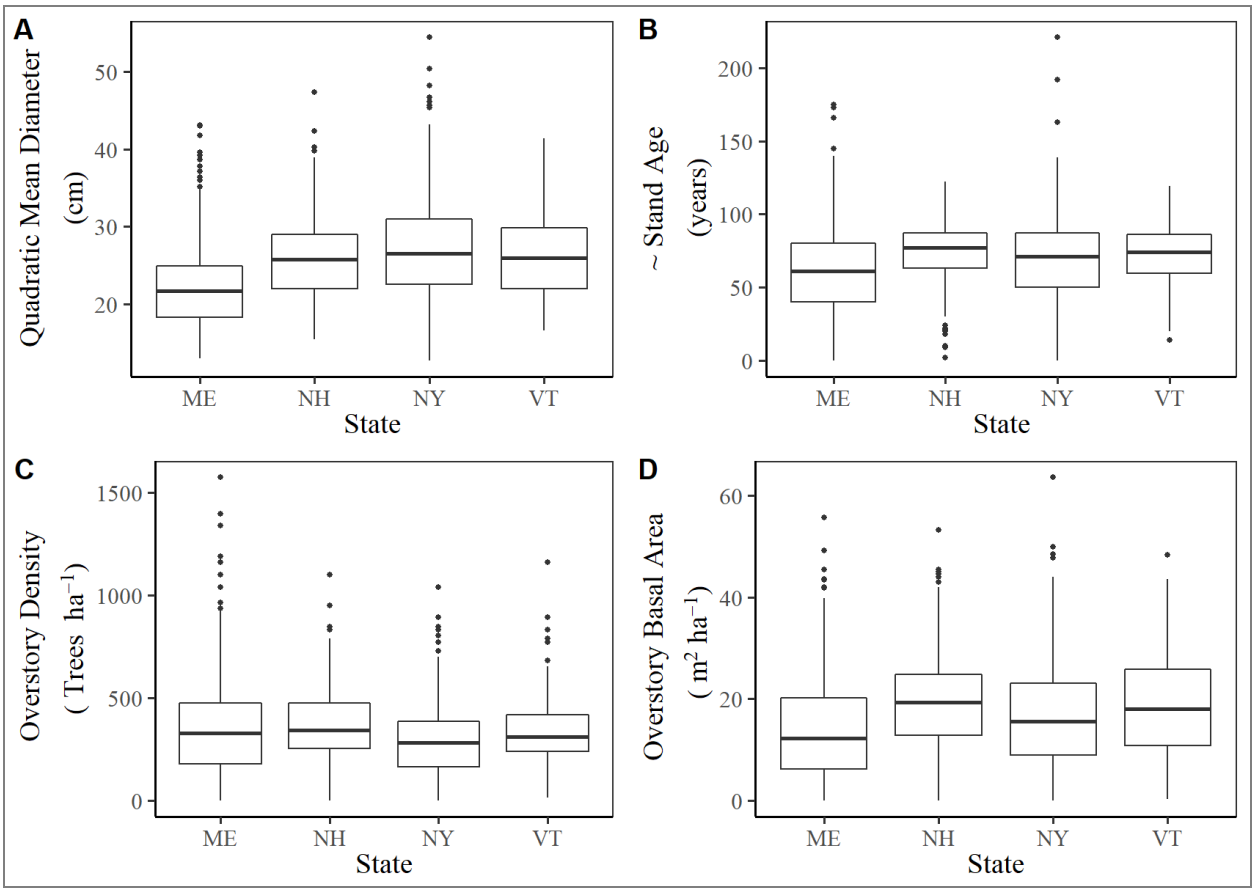

Figure 1-3. Average overstory attributes by state, A: quadratic mean diameter, B: approximate stand age, C: overstory density, D: overstory basal area.

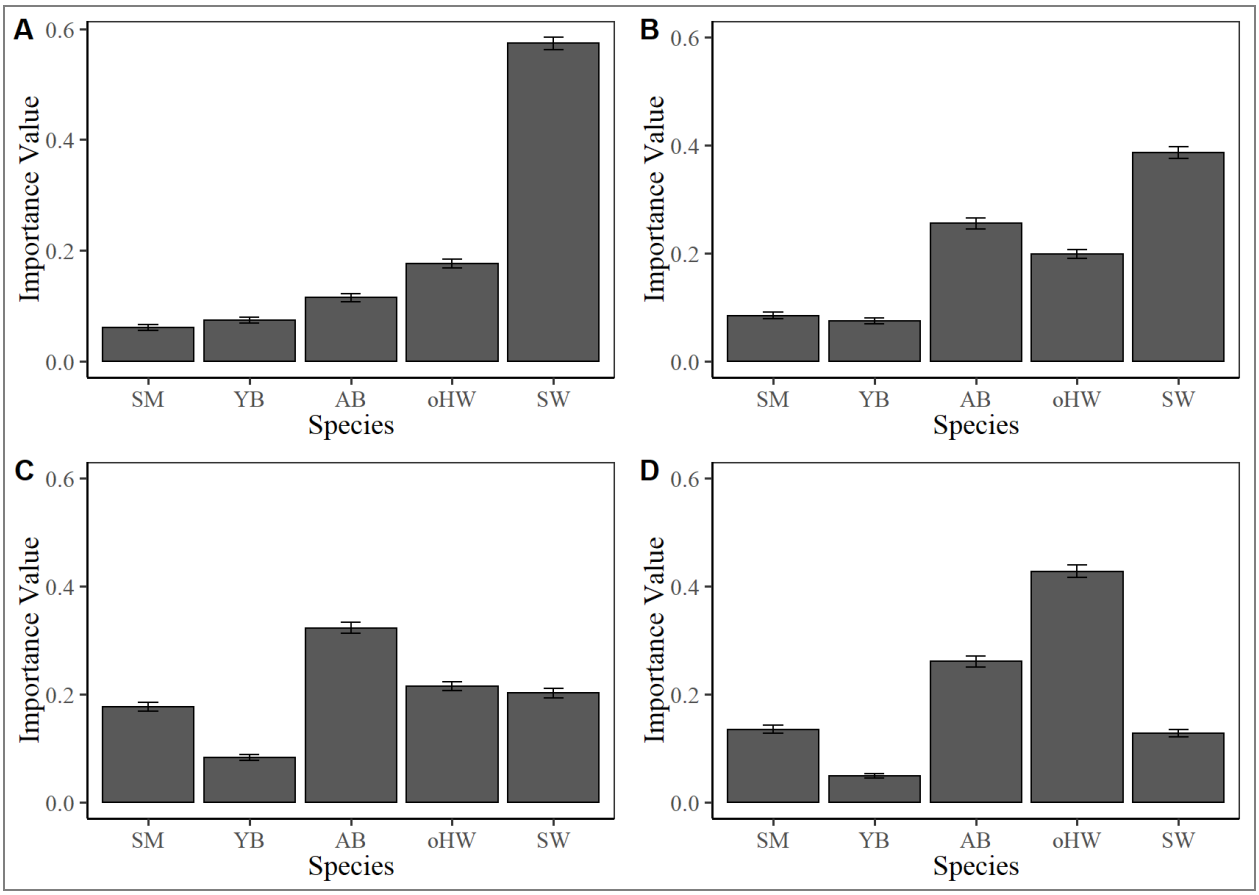

Figure 1-4. Advance regeneration species importance values by state, A: Maine, B: New Hampshire, C: Vermont, D: New York.

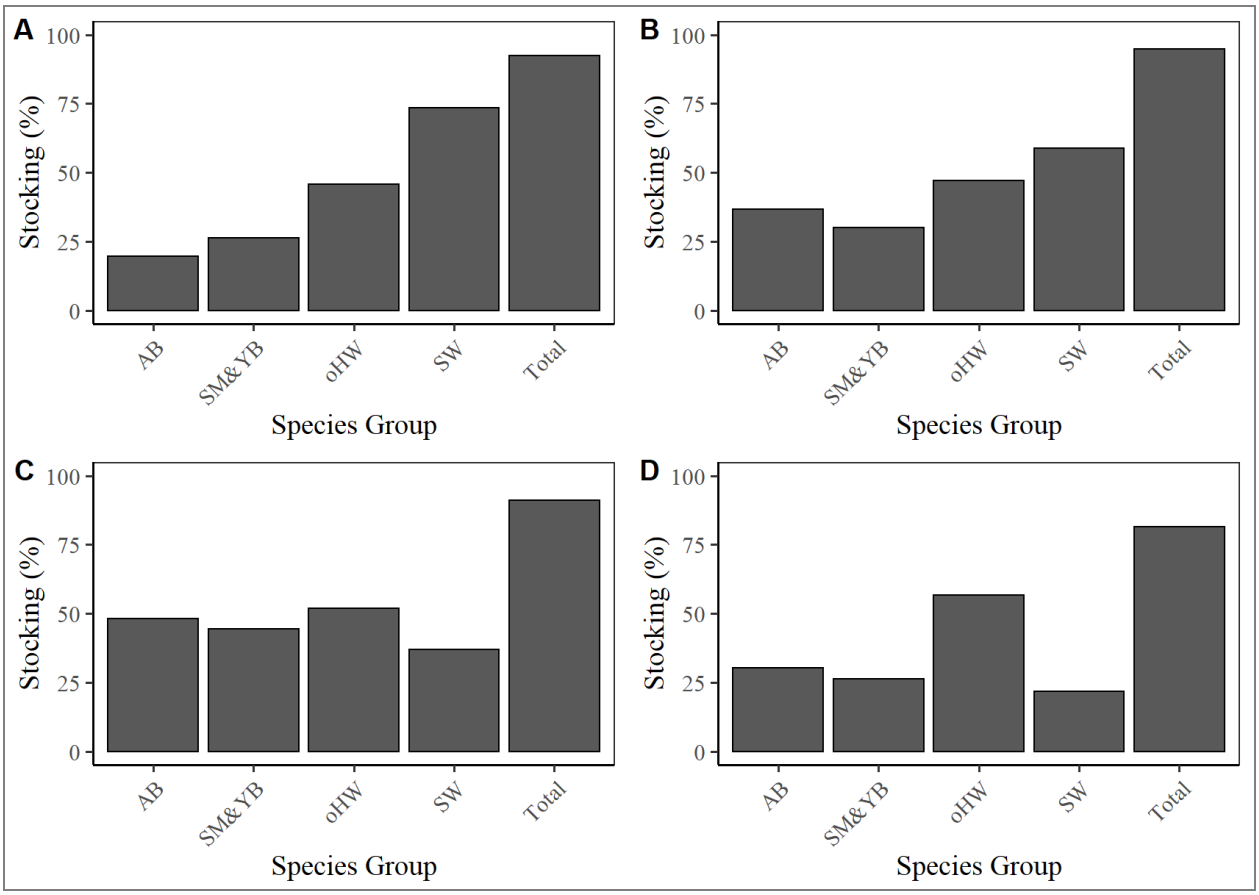

Figure 1-5. Stocking of advance regeneration by species group and state, A: Maine, B: New Hampshire, C: Vermont, D: New York.

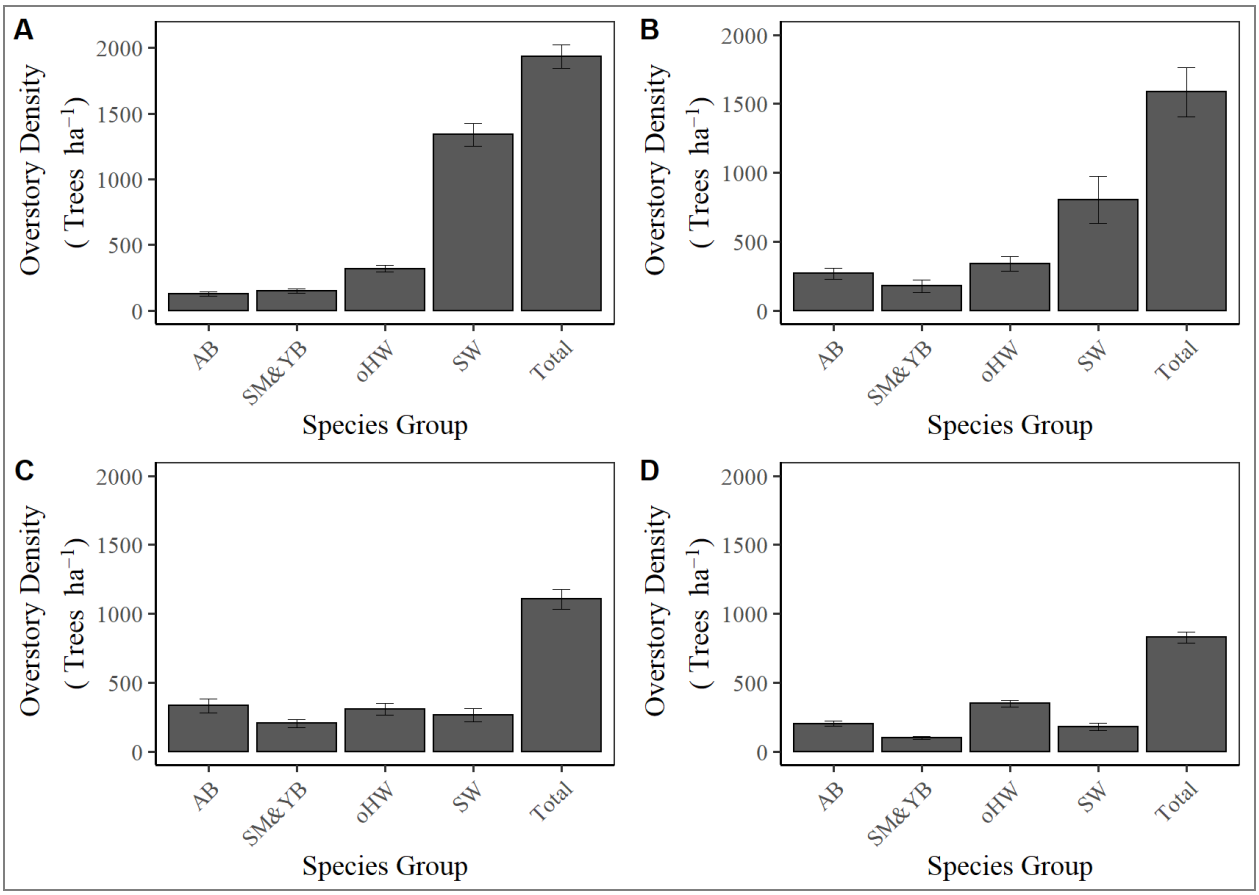

Figure 1-6. Density of advance regeneration by species group and state, A: Maine, B: New Hampshire, C: Vermont, D: New York.

CHAPTER 2: IDENTIFYING FACTORS AFFECTING REGIONAL PATTERNS OF SUGAR MAPLE REGENERATION IN THE NORTHERN NEW ENGLAND AND NEW YORK.

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2.1 Abstract

Sugar maple (*Acer saccharum* Marsh.) is an economically, ecologically, and culturally important component of northern hardwood forests in the northeastern United States. Site-level studies throughout the region suggest sugar maple regeneration may be in extreme decline. This decline has been attributed to changes in a variety of biotic and abiotic factors, including white-tailed deer (*Odocoileus virginianus*) herbivory, competition from American beech (*Fagus grandifolia* L.) unfavorable site conditions, and past harvesting practices. Despite documented site-level declines, key knowledge gaps remain regarding how these patterns manifest over broad spatial scales, limiting effective management for future sugar maple-dominated forests across this region. To capture regional patterns in sugar maple reproductive success, we compiled inventory data from managed and unmanaged stands throughout Maine, New Hampshire, Vermont, and New York. Utilizing random forest methodology, we identified the relative importance of variables driving sugar maple regeneration throughout the Northern Forest.

Findings expand on past site-level studies and suggest abundance of American beech saplings and characteristics capturing the physical location of sites, including elevation, latitude, and longitude, are most influential in affecting successful sugar maple establishment. Aspects of regeneration success across the region remained largely unexplained by a host of examined variables; however, general findings underscore the increasing importance of treatments focused on controlling American beech in conjunction with evaluating suitability of site-level conditions to sustain sugar maple-dominated forests across the region.

2.2 Introduction

Sugar maple (*Acer saccharum* Marsh.) is an important species commonly found in the hardwood forests of the northeastern United States. Grown on approximately 12.5 million ha, sugar maple is an economic staple in local forest products markets, valued for quality lumber and specialty items (Burns and Honkala 1990, Godman and Mendel 1978). The species is also regarded for its vibrant fall foliage and the high sugar content of its sap used in maple syrup production (Houston, 1999). For example, in Vermont, the largest national producer of maple syrup, the industry netted between $317 and $330 million in sales in 2013 alone (Center for Rural Studies 2013).

Beyond providing significant derived commodities for the region, sugar maple is also associated with many ecological benefits throughout the northern hardwood forest. Relative to other common canopy tree associates, sugar maple has greater impact on nitrogen cycling rates and levels of nitrogen retention in forested watersheds (Lovett and Mitchell, 2004). The high calcium content in sugar maple foliage has also been correlated with increased levels of this cation in soils at local scales (Lucash et al., 2012).

Sugar maple is also a valuable species from a wildlife habitat perspective. In the Adirondack region of New York, researchers reported a positive association between roost selection for the federally endangered Indiana bat (*Myotis sodalisa*) and increased presence of sugar maple (Jachowski et al., 2016). In Pennsylvania, fisher cats (*Martes pennant*) were observed favoring sugar maple cavity trees for den sites (Gess et al. 2003). Given the high economic, ecological, and cultural value of this species, a large volume of work over the past century has been devoted to exploring the influence of biotic and abiotic drivers on sugar maple growth and development (Jacobs 1969; Nyland 1999, 2005; Duchesne et al. 2005). In recent decades, numerous studies have also documented declines in sugar maple health and occurrence (Beaudet et al. 1999; Duchesne et al. 2005; Hartmann et al. 2009). This decline, inclusive of regeneration, is especially concerning as silvicultural systems applied to forests in the northeast rely almost exclusively on natural regeneration methods (Seymour 1995; Brissette 1996). Variability in density and stocking of natural regeneration is to be expected across large spatial scales; however, recent trends suggest a broader decline in sugar maple regeneration with several potential causative factors identified, including unfavorable site conditions, competition from American beech (*Fagus grandifolia* L.), elevated white-tailed deer (*Odocoileus virginianus*) populations, and past harvesting practices.

Sugar maple is a temperate, shade-tolerant species best grown on rich, well drained soils (Godman et al. 1990). On fine tills or areas of soil enrichment, such as toe slopes, sugar maple can be highly competitive and maintain long-term dominance (Leak, 1991). However, as site quality decreases, such as on sandy tills or at higher elevations, beech outcompetes sugar maple in the absence of canopy disturbance (Leak 1987; Leak

1991). Nutrient availability can also influence the longevity and establishment of sugar maple. Low levels of calcium, magnesium, manganese, and nitrogen are stressors that can predispose sugar maple to declining growth (Halman et al., 2015; Long et al., 2009). Acid rain, attributed to elevated air pollution, has been linked to accelerated leaching of these nutrients from forested systems in the Northeast (Likens et al., 1996; Likens and Bormann, 1974), with fertilization treatments on these depleted sites demonstrating positive effects on survival of sugar maple seedlings relative to untreated sites (Cleavitt et al., 2011). In addition to site quality and nutrient levels, soil moisture can be an important factor for regeneration success. Sites with overly saturated soils pose a greater risk for regeneration failure as excess moisture can inhibit soil aeration and thus growth (Marquis et al. 1992). However, sugar maple seedlings are also sensitive to drought conditions and seedling survivorship declines during drought years if access to soil moisture is limited (Hane, 2003; Hett and Loucks, 1971).

Although certain site characteristics may predispose regeneration success or failure, these site conditions often interact with levels of competition from other species, particularly beech, to affect sugar maple regeneration dynamics. Following introduction of beech bark disease complex, (*Cryptococcus fagisuga* and *Neonectria spp.)* from Nova Scotia in the 1890s, most mature beech in the Northeast has been replaced by small, dense clusters of beech suckers over the past century (Shigo 1972; Houston 1975, Cale et al. 2017). Beech is extremely shade tolerant and can outcompete sugar maple for years at low light levels unless manually removed or treated with herbicide application (Nyland et al. 2001; Bohn and Nyland 2003; Sage et al. 2003). Beech thickets may also reduce the growth of sugar maple saplings and seedlings through competition for below ground

resources (Hane 2003), as well as through potential phytotoxic effects due to secondary compounds in its leaf litter (Hane et al., 2003; Leak, 2005; Leak et al., 2006). Competitive interactions between American beech and more economically desired species such as sugar maple are further exacerbated by heavy browse pressure from white-tailed deer (Marquis et al. 1992). Relative to maple, beech is much less palatable and only exposed to light browsing (Tierson et al., 1966). For example, Sage et al. (2003) found establishment of desired hardwood regeneration was controlled largely by three components: the forest light regime, interaction with competing species, and browsing by white-tailed deer. Similar results were observed in West Virginia where high deer populations, 11.5 to 18 deer/km^2, negated the positive influence of light availability from large gaps on species diversity (Nuttle et al., 2013). If left unchecked, heavy browsing will shift species composition on a site from sugar maple to beech dominance or other commercially undesirable understory species (Kelty and Nyland 1981; Cote et al. 2004; Nyland et al. 2006).

In the northern hardwood forests, sugar maple can regenerate well under both even and uneven-aged silvicultural systems (Bédard and Majcen, 2003; Tubbs and Metzger, 1969), depending on site conditions and associated cultural treatments focused on controlling for beech competition and herbivory (Kelty and Nyland, 1981; Leak et al., 1988; Nyland et al., 2006). Long-term research across the range of northern hardwoods has demonstrated successful regeneration and increased stand quality with careful application of single-tree selection, especially with efforts for beech control and reduction of deer browse impacts (Jones et al., 1989). Group selection and patch selection, in which all pre-existing beech are felled during regeneration harvests, are also commonly applied

silvicultural system, which relative to single-selection have demonstrated increased species diversity by providing the light levels necessary to allow comparatively less tolerant species, including sugar maple, a competitive advantage over beech populations (Leak and Filip, 1977; Leak, 1999). In areas of high deer populations, patch selection using large openings (0.2 to 2 ha) can be a successful means of management by creating more forage than deer can consume, creating higher odds of survival for regenerating sugar maple and other desired hardwoods (Marquis 1992).

Yet, just as thoughtful silviculture can favor sugar maple establishment, poor management can also inhibit the species. Several studies have demonstrated that diameter-limit cutting and other forms of high grading can limit sugar maple seedling and sapling survival (Kenefic and Nyland 2005). Maintaining sugar maple within a stand or landscape for the long-term requires cultivation and protection of advance regeneration (Nyland, 1992). However, high grading disregards the spatial location of advance regeneration when removing quality products from the site (Kenefic and Nyland, 2006). While diameter-limit cutting may remove enough volume to create light conditions where sugar maple can be regenerated, without careful tending of advance regeneration, success of seedlings and saplings following this practice has been inconsistent (Nyland, 1992). Much of what we know about sugar maple regeneration dynamics, as well as drivers of regeneration failure, has been learned from intensively measured, local studies. However, this approach leaves uncertainty about seedling and sapling establishment and survival at the regional scale. The main goal of this work was to identify factors influencing sugar maple regeneration broadly across hardwood forests of the northeast while providing a unique opportunity to consider existing knowledge across a gradient of

biotic and abiotic conditions. We hypothesize that local drivers identified in previous work can be detected over the broad extent of northern hardwood forests using Random Forests techniques applied to regional datasets and forest inventories.

2.3 Materials and Methods

2.3.1 Study Area

The study area for this research is the region encompassed by northern hardwood forests in Maine, New Hampshire, Vermont, and New York. The region is humid and cool, with average annual precipitation between 80 to 130 cm and an elevation range of 150 to 460 m. Soils throughout the study area can be quite variable, but are generally classified as podzols (Seymour 1995). Private ownerships are the dominant ownership type, ranging from small family woodlot owners to large, industrial and investment owners (Hewes et al. 2014).

Dominant species in the northern hardwood forest are sugar maple, American beech, and yellow birch *(Betula alleghaniensis* Britton). Other common associates include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), and white ash (*Fraxinus americana* L.). Small components of northern conifers such as red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and balsam fir (*Abies balsamea* L.), may also be present.

Data

To meet the objective of this work, data were obtained from the U.S. Forest Service Forest Inventory Analysis program (FIA) (https://fia.fs.fed.us). FIA is a national census comprised of a network of permanent sample plots established on a grid system across the United States. Plot design is four, circular 7.2 m radius subplots with nested

micro-plots using a radius of 2 m. All trees ≥ 12.7 cm DBH are measured on subplots, while saplings (2.5 to 12.4 cm DBH) and seedlings (< 2.5 cm DBH, height ≥ 15.2 cm for softwood species, ≥ 30.4 cm for hardwood species) are measured on micro-plots. Plots are re-measured on an approximately 5-year cycle (USDA 2007). For this work, plots included in analysis had composition of overstory sugar maple ≥ 20% by basal area to ensure sugar maple sites (Leak et al., 1987) and were measured between 2003 and 2015.

2.3.2 Response and Explanatory Variables

Two response variables were calculated for this analysis, *sugar maple sapling density* (stems ha^{-1}) and *sugar maple seedling density* (stems ha^{-1}). Separating seedlings and saplings into two variables allowed us to explore the relationships influencing regeneration establishment (seedlings) and regeneration success (saplings).

Twenty potential explanatory variables were evaluated based on previous findings from site-level studies on sugar maple recruitment and comprised six categories representing understory structure and composition, overstory structure and composition, site characteristics, climate, soil characteristics, and site history (Table 1). Variables were derived from downloaded FIA data, except for climate and soil characteristic variables. Climate variables were extracted from raster files of monthly PRISM data (http://prism.oregonstate.edu/) and soil variables were extracted from STATSGO digital soil maps (https://www.nrcs.usda.gov). Variable extraction was completed in ArcGIS. Estimates of white-tailed deer density for the study area were not available at the plot level, so we were unable to include explanatory variables representing deer densities or browsing in our analysis. However, deer density data from Walters et al. (2016) were

used to create Figure 1 and provide visual assessment of regional deer populations on sugar maple seedling density.

2.3.3 Random Forest Analysis

Random forest analysis (RF) was used to evaluate the importance of potential explanatory variables in predicting sugar maple sapling and seedling density. RF is a nonparametric statistical tool based on regression and classification trees with the flexibility to compare multiple data types (Breiman 2001). The complex nature of our data as well as nonlinear relationships between explanatory variables and the response variables made RF a more effective tool than other statistical methods such as generalized linear regression (Cutler et al., 2007; Oliveira et al., 2012).

For RF, “forests" are constructed from a combination of unique predictive trees (Breiman 2001). At each split, for a given tree, a subset of explanatory variables is randomly selected with further randomness incorporated into the forest using bootstrapping. The original dataset is split with two thirds of the data for model construction, called the in-bag-sample, and the remaining third of the data, called the out-of-bag sample (OBB), retained for model validation (Breiman, 2001; Liaw et al., 2002). The final model is an average of all trees within the forest, reducing the likelihood of overfitting, a common challenge for traditional regression trees.

Using variable importance plots, the influence of each explanatory variable in the overall model was ranked by percent increase in mean square error (%IncreaseMSE). In RF, %IncreaseMSE measures the overall increase in MSE when a given variable is

removed and the model is run on the OBB sample (Breiman 2001; Liaw and Wiener 2002).

RF regression was performed for sugar maple sapling and seedling density on all plots (n = 3575). Additionally, data were subset to plots classified as having adequate sapling density (n = 225) and seedling density (n = 370) and RF was then run again. For saplings, adequate regeneration was defined as plots with sugar maple density ≥ 865 stems ha^{-1} based on guidelines from the Vermont Use Value Program (http://fpr.vermont.gov). Adequate seedling density was classified as sugar maple density ≥ 1850 stems ha^{-1} using recommendations from Marquis et al. (1992). Moving forward seedling density data from all plots will be referred to as SEEDall, sapling density from all plots as SAPall, adequate seedling density as SEEDadeq, and adequate sapling density as SAPadeq.

Analysis was completed using the R statistical software version 3.2.3 (https://www.r-project.org/) with the package randomForest and the function randomForest (Liaw and Wiener. 2006). A random number generator, seed, was set to 2016 to keep results reproducible. Partial dependence plots were used to explore the relationship between select explanatory variables and sugar maple seedling and sapling density. Partial dependence plots, based on the RF model, are an interpretive tool showing the trend of a selected explanatory variable against the predicted value of the response variable from the RF model (Friedman 2001). For regression analysis, the y-axis is the average predicted value of our response variables, which were either sugar maple seedling or sapling density.

2.4 Results

2.4.1 All Plots

For SEEDall, density of other seedlings was an important predictor in regeneration establishment (Figure 2A). Other top explanatory variables for sugar maple establishment were related to the physical location of plots, longitude, latitude, and elevation. These variables all had a VIF with a %IncreaseMSE ≥ 20. For SAPall, seeding and sapling density of other species, as well as latitude, were the most important variables for explaining patterns in regeneration success, again with a %IncreaseMSE ≥ 20 (Figure 3A).

For seedling analysis, partial dependence plots (PDP) showed a decreasing dependence between sugar maple seedlings and increasing density of other seedlings (4A). Sugar maple seedlings showed generally increasing partial dependences with increases in site level variables including longitude, latitude, and elevation (Figure 4B, C, and D).

For SAPall, PDPs for variables with a %IncreaseMSE ≥ 20 showed a positively increasing relationship with density of other saplings and sugar maple seedling density (Figure 5A and C). The partial dependence between sugar maple saplings and beech seedling and sapling density had an initial sharp decline followed by a plateau at higher beech density (Figure 5D and F). For latitude, the partial dependence between sugar maple sapling density was variable (Figure 5E).

2.4.2 Adequate Regeneration

On plots with adequate seedling establishment, SEEDadeq, the most important variable was latitude and no variables had a %IncreaseMSE ≥ 20 (Figure 2B). For sapling regeneration, SAPadeq, density of other saplings, excluding beech and sugar maple, was the most important explanatory variable (Figure 3B), and the only variable with %IncreaseMSE ≥ 20.

For SEEDadeq, there was a positive dependence with beech seedlings and slope (Figure 6B and C). The partial dependence between seedling density and latitude, longitude, and biomass of downed woody debris were variable (Figure 6A, D, and E). PDPs for SAPadeq showed increasing dependence between sugar maple sapling density with increasing values of other sapling density and slope and a decreasing dependence with increasing values of aspect and Shannon's diversity (Figure 7A -D). The partial dependence between sugar maple sapling density and longitude was variable (Figure 7E).

2.5 Discussion

The northern hardwood forests of New England and New York are diverse and cover a wide range of biotic and abiotic conditions. The results of this study reflect the variability of the region. Yet, despite the complex interaction of factors influencing sugar maple regeneration, some trends emerged that were consistent with past site-level investigations and further underscored the pervasive regional influence of factors, such as American beech competition, on the sustainable management of sugar maple forests. The variable importance plots for seedlings revealed a number of key site-level factors (i.e., physiographic attributes of individual FIA plots) that were very important to sugar maple establishment, including latitude, longitude, and elevation (Figure 2). These

variables may directly influence seedling density but more likely capture many interacting factors important to sugar maple regeneration. Additionally, other studies in the northeast have noted the dynamic nature of the regeneration stage (Hibbs 1983) and it is not unexpected to see some level of unexplained variability. In the Lake States, a decline in sugar maple seedling and sapling density with decreasing latitude was interpreted as reflecting less regeneration at sites with lower snow pack and greater deer populations (Matonis et al. 2011). In this study, the combination of latitude, longitude, and elevation could represent distinct site features like soil quality. For a species such as sugar maple which favors enriched sites, slight changes in soil characteristics could alter percent composition and growth (Leak, 1978; Nyland, 1999). Throughout the species' range, Kobe et al. (1995) saw higher abundance of sugar maple saplings when soils were calcareous vs. acidic (1995). Leak (1990) observed that successional dynamics and dominant species on a site were also closely guided parent material (1990). Yet, despite the known relationship between soil attributes and sugar maple abundance, soil variables directly included in our analysis were not highly ranked. The low %IncreaseMSE for soil depth, pH, and water availability in the model may be a reflective of the coarse nature of the data used for these variables. Regional soil maps are a valuable data source, but may not capture the fine scale variability of soil properties (Lathrop and Aber, 1995). In this context, variables representing the physical location of plots may have summarized this fine scale soil variability more effectively.

At the sapling layer, variables identified as important are also likely representing more complex and interacting relationships. For SAPall and SAPadeq, the positive relationship with density of other saplings (Figure 5A and 7A) could represent overall

favorable conditions for regeneration at a site, i.e. where conditions are improved for regeneration as a whole there will also be an increase in sugar maple saplings. Adequate light availability in the understory is one such condition that favors sapling growth across all species, including sugar maple. Beaudet et al. (1999) attributed regeneration failure in an old-growth stand relative to a managed stand to limited microsites with ample light availability, rather than lack of recruitment (1999). We attempted to include light availability into the analysis using basal area and stand density as surrogates, but microsite may be more accurately represented by total regeneration density. The sapling stage is also more likely to express the dynamics of a given species than the seedling stage. In New Hampshire, Leak (1979) found composition of hardwood saplings was largely the product of available seed sources and chance with known relationships between habitat attributes and species composition not becoming apparent until the stand moved towards poletimber size classes(1979).

Density of white-tailed deer is an additional factor impacting sugar maple regeneration that can vary considerably between sites. Campbell et al. (2004) found deer populations can fluctuate in areas < $2km^2$ based on local management and the home range of matriarchal social groups. In Figure 1, visual assessment suggests fewer plots with sugar maple regeneration where deer densities exceed 39 km^2 based on data from Walters et al. (2016; Figure 1). However, these results need to be considered within the scale of the available data. In New York, deer density was not influential to sugar maple regeneration success at spatial scales above 10,000 m^2 (Didier and Porter, 2003). The authors attributed this weak relationship, in part, to importance of multiple interacting factors, rather than one primary driver in regeneration success (Didier and Porter 2003).

One such factor that may interact with deer browse is the density of competing understory vegetation. Horsley and Marquis (1983) observed that regeneration struggled to outgrow surrounding grasses and ferns on sites with dense understory vegetation, and what seedlings did succeed were browsed back unless deer enclosures were used. Browsing of more palatable species, such as sugar maple, also frees up growing space of less browsed species, like beech, creating an interactive effect between deer densities and competition between species (Horsley et al. 2003). While we did include some measures of these variables individually, including beech and species competition, it was difficult to capture these multipart relationships at the regional scale.

Competition from American beech was also directly detected in the RF analysis and observed to have a negative effect of sugar maple saplings (Figure 5D, 5F). The lack of influence of beech on sugar maple seedlings (Figure 2) suggests that other factors are more restrictive to establishment, but beech competition creates a bottleneck between seedlings and sapling survival. Numerous studies have documented the negative competitive dynamics between beech regeneration and sugar maple (Bohn and Nyland, 2003; Bose et al., 2017a; Nyland et al., 2006; Ostrofsky, 2005), although the degree of competition may vary. Advance regeneration of sugar maple and beech both respond to small canopy gaps, but beech growth is higher under closed canopies (Canham 1988, 1989). Beech suckers also promote more abundant regeneration in dense shade where sugar maple must establish from seed (Beaudet et al. 1999). The positive relationship between adequate sapling densities and density of other saplings, excluding beech and sugar maple, may suggest sugar maple remains competitive on sites with canopy gaps large enough to recruit less tolerant species (Figure 5). Light availability can further

interact with soil quality and local deer populations to hinder sugar maple regeneration (Collin et al., 2017; Leak, 1979). Variables compounding the effect of beech competition may be best addressed at the stand scale, however, these results emphasize the necessity of beech management throughout the range of sugar maple in the northeast.

This work did not explicitly include the influence of different silvicultural systems or management activities, although basal area, stand density, and species composition of each plot may allude to past management. Silvicultural systems would certainly influence the establishment and success of sugar maple, in addition to other species. Single-tree selection, which promotes more shade tolerant species, works well on rich sites where sugar maple can out compete other species, and/or in conjunction with beech control (Jones et al. 1989, Bedard and Majcen 2003, Nyland et al. 2006). On more moderate sites, group selection has increased the composition of desired species, including sugar maple, relative to beech (Leak and Filip 1977, Leak 1999, Webster and Lorimer 2002). However, both treatments require attention to regeneration, as new cohorts must be established at each entry (Leak et al. 2014). Even-age management can be another tool for management of sugar maple. In northern New York, uniform shelterwood cutting and chemical control of beech, successfully regenerated yellow birch and sugar maple in areas where deer populations had been reduced through targeted hunting (Kelty and Nyland, 1981).

For this analysis we did not directly consider abundance of seed sources or occurrence of seed years. However, FIA plots were restricted to those with sugar maple composition $\geq 20\%$ by basal area. By only considering these plots, we assumed that ample seed sources were present during the study period. Additionally, characterization

of plots with adequate regeneration were based on guidelines that were not species specific. As such, our definition of adequate regeneration may be liberal when only considering sugar maple. For example, only 6.3 % of all plots measured had adequate levels of sugar maple saplings and 10.3% of plots had adequate sugar maple seedling density.

The period of interest for this work was from 2002 to 2013, and it is important to note that attributes influencing regeneration success may shift with changing climatic conditions in the future. Partial dependence plots for sugar maple seedlings and saplings showed some variability along gradients of longitude and latitude (Figure 5E, 4B, 4C, 7E, 6D) although higher densities of seedlings and saplings were both found at higher latitudes and longitudes. Observations from U.S. Forest Service climate change models show the range of sugar maple may move north, although the extent of this range shift will depend on the severity of climate change and associated events (https://www.fs.fed.us/nrs/atlas/).

The importance of site in affecting establishment and growth of sugar maple regeneration needs to be considered in light of projected changes in climate conditions and prevalence of invasive species. Weather conditions and events that may alter how successful sugar maple is on a site include late or variable snow pack and increased drought events. In New Hampshire, warming winters disrupted snowpack and, despite warmer air temperatures, there were higher instances of soil freezing and damaged fine roots (Groffman et al. 2002). Fine root damage could reduce nutrient mineralization and uptake, which is important for seedling survival (Tierney et al. 2001). Relative to other species such as yellow birch, sugar maple roots are more susceptible to fine root damage

(Calme et al. 1994). Increased drought events could be detrimental to regeneration establishment and survival, especially for species such as sugar maple that require mesic conditions (Allen et al. 2010, Dale et al. 2001). Invasive species may also shift regeneration dynamics in the future. One such suite of species are non-native European earthworms (e.g. *Lumbricus terrestris*). In the Lake States, invasive, European earthworms are attributed with the disappearance of leaf litter essential to germination and establishment of sugar maple regeneration (Augustine et al. 1998 and Hale et al. 2006).

2.6 Conclusions

This work underscores the complex nature of sugar maple reproductive success and the need for thoughtful management to maintain and promote the species throughout New England and New York. Using RF analysis, we demonstrated the negative influence of American beech competition on sugar maple regeneration at regional scale. These findings support continued control of beech on sites where sugar maple is the desired species. Additionally, this work highlights that the dynamic nature of the regeneration stage can be difficult to capture directly. Maintenance of sugar maple as long-term component of northern hardwood forests likely relies on management that considers site level attributes and operations that utilize existing sugar maple regeneration.

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Figures

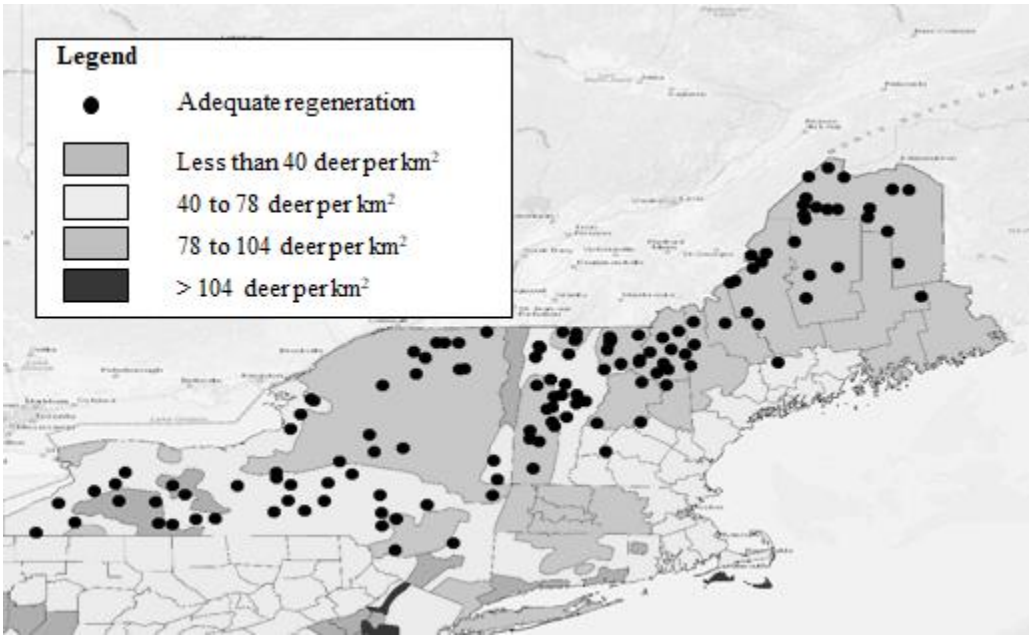

Figure 2-1.Regional deer densities and sugar maple seedling density.

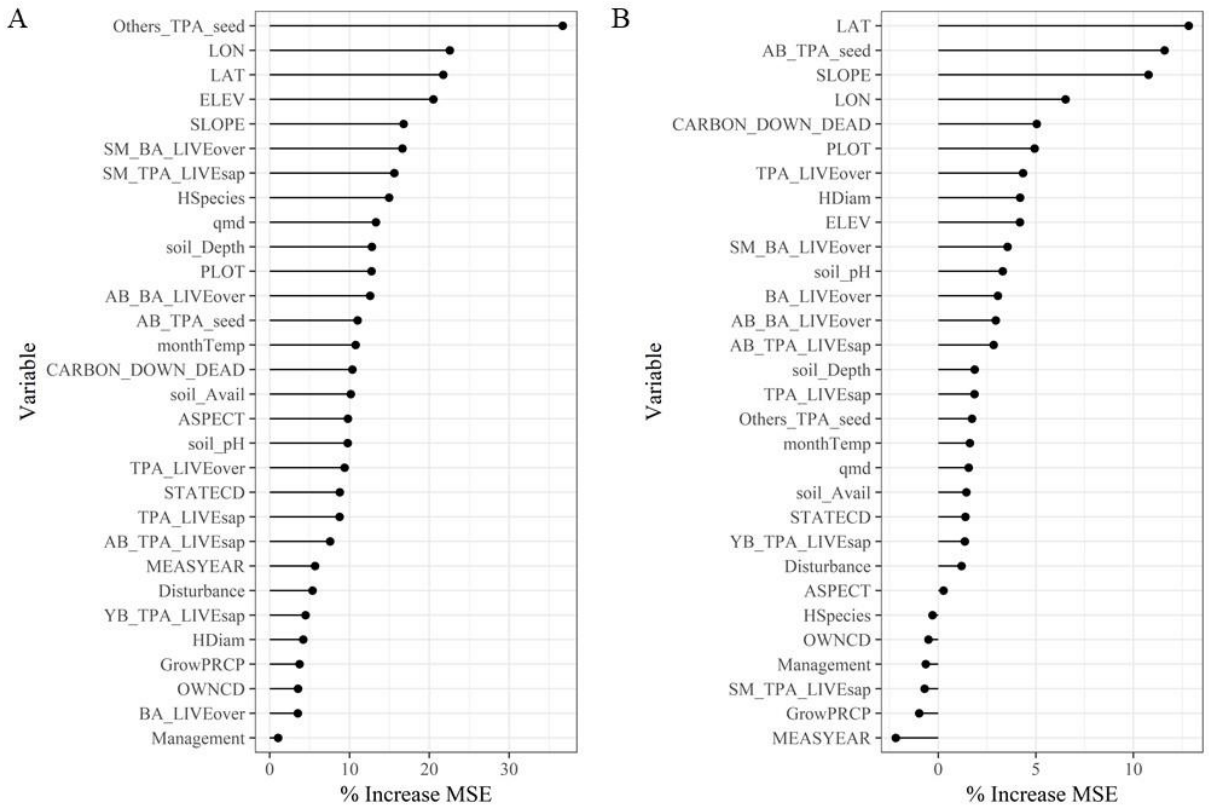

Figure 2-2. Variable importance plots from random forest for sugar maple seedlings. A) All FIA plots, B) FIA plots with adequate regeneration.

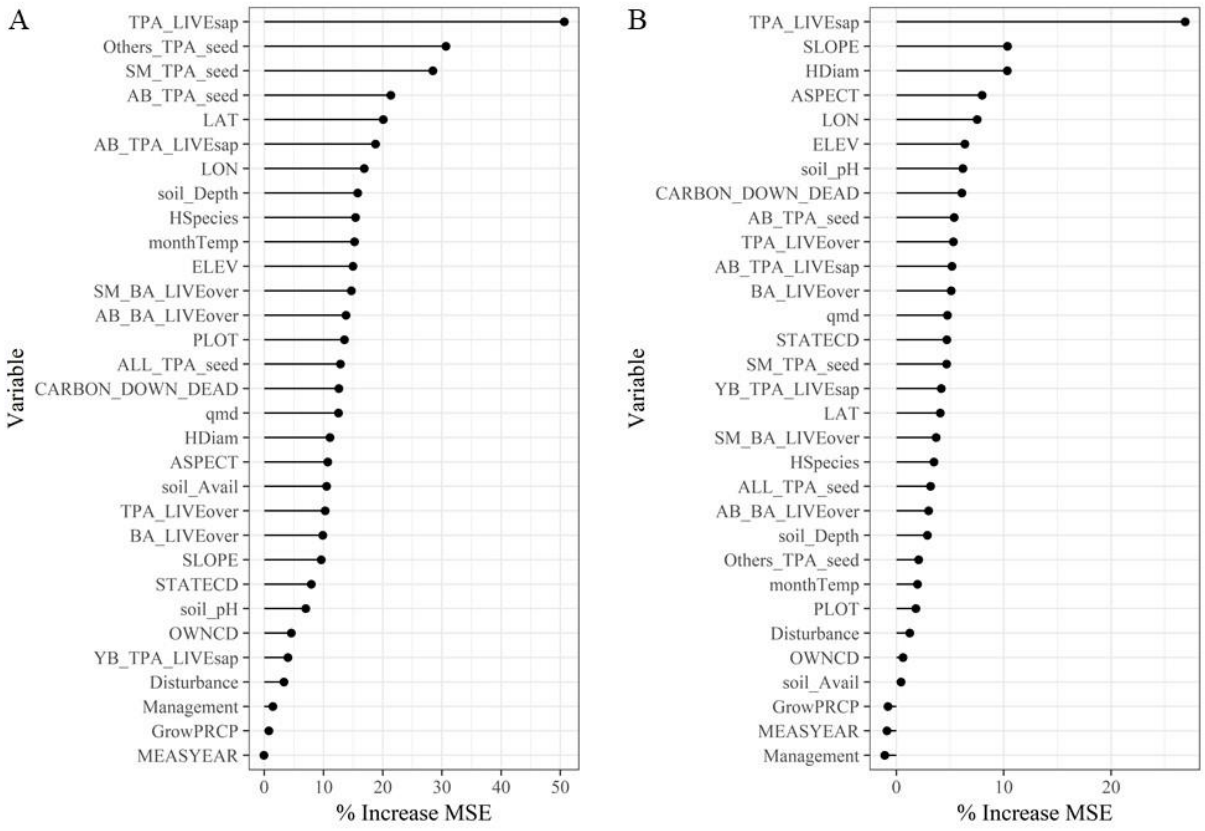

Figure 2-3. Variable importance plots from random forest for sugar maple saplings. A) All FIA plots, B) FIA plots with adequate regeneration.

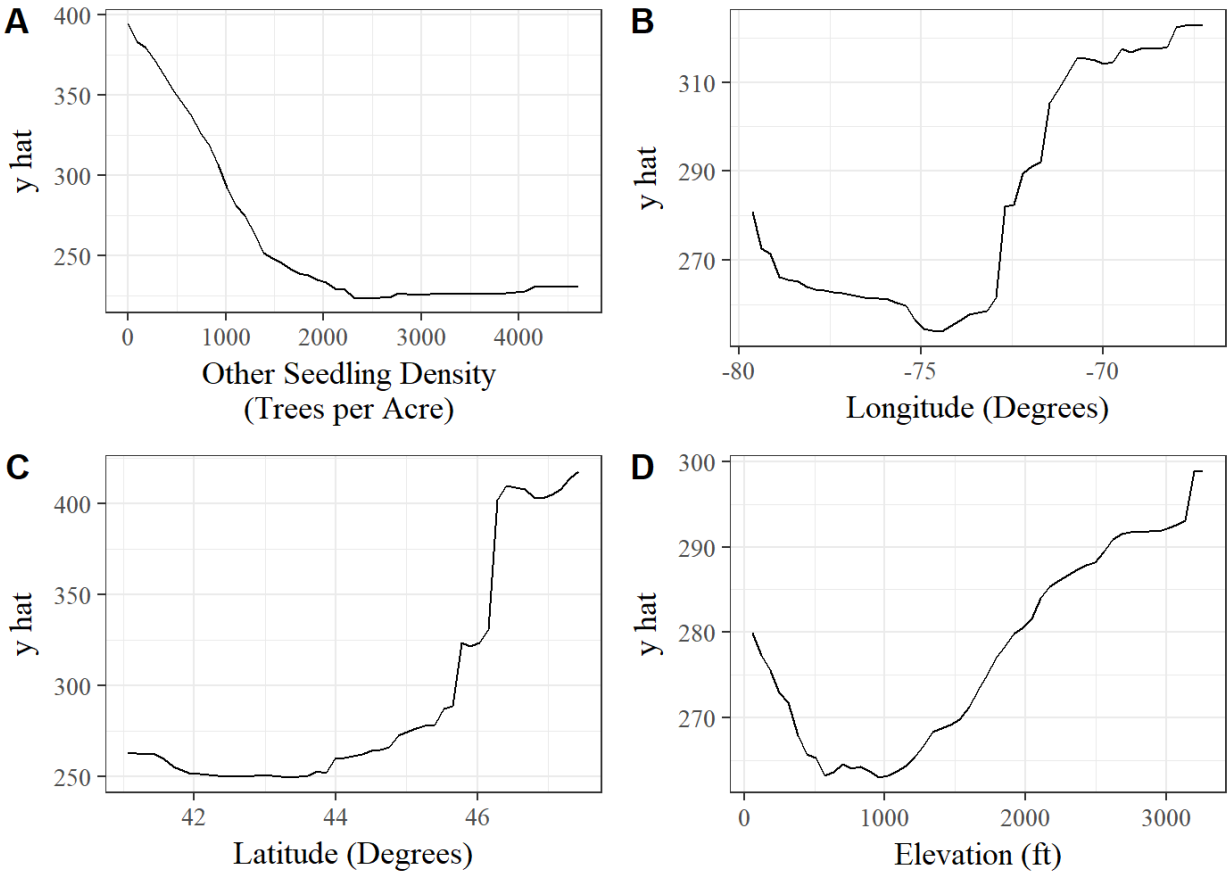

Figure 2-4. Partial dependence plots for sugar maple seedling density on all plots. Included variables were those with % Increase MSE ≥ 20.

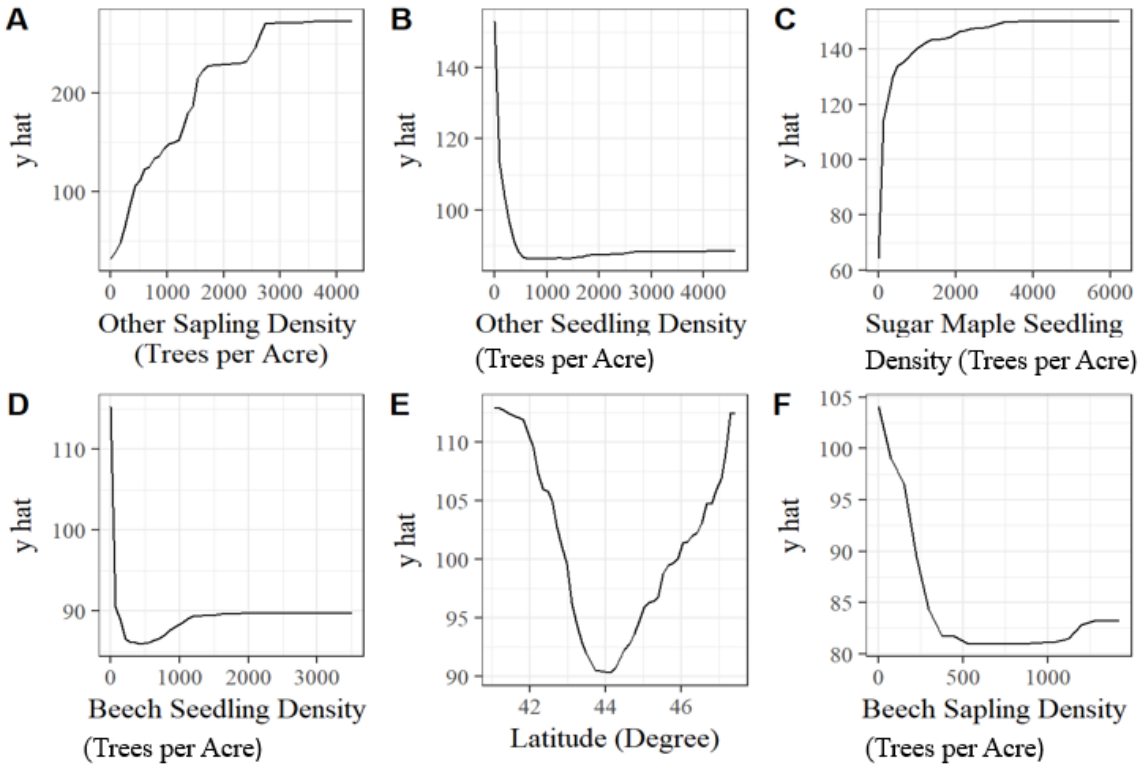

Figure 2-5. Partial dependence plots for sugar maple sapling density on all plots. Included variables were those with % Increase MSE ≥ 20.

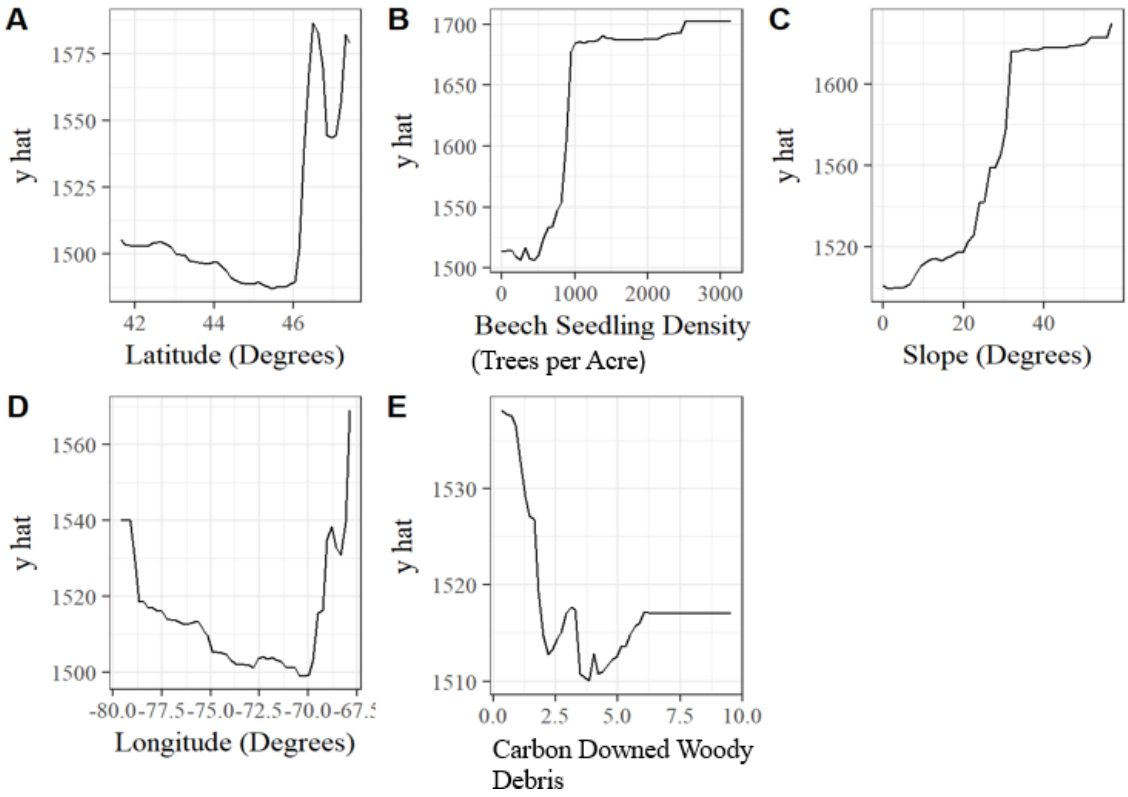

Figure 2-6. Partial dependence plots for sugar maple seedling density on all plots with adequate regeneration. These were the top five variables in the model.

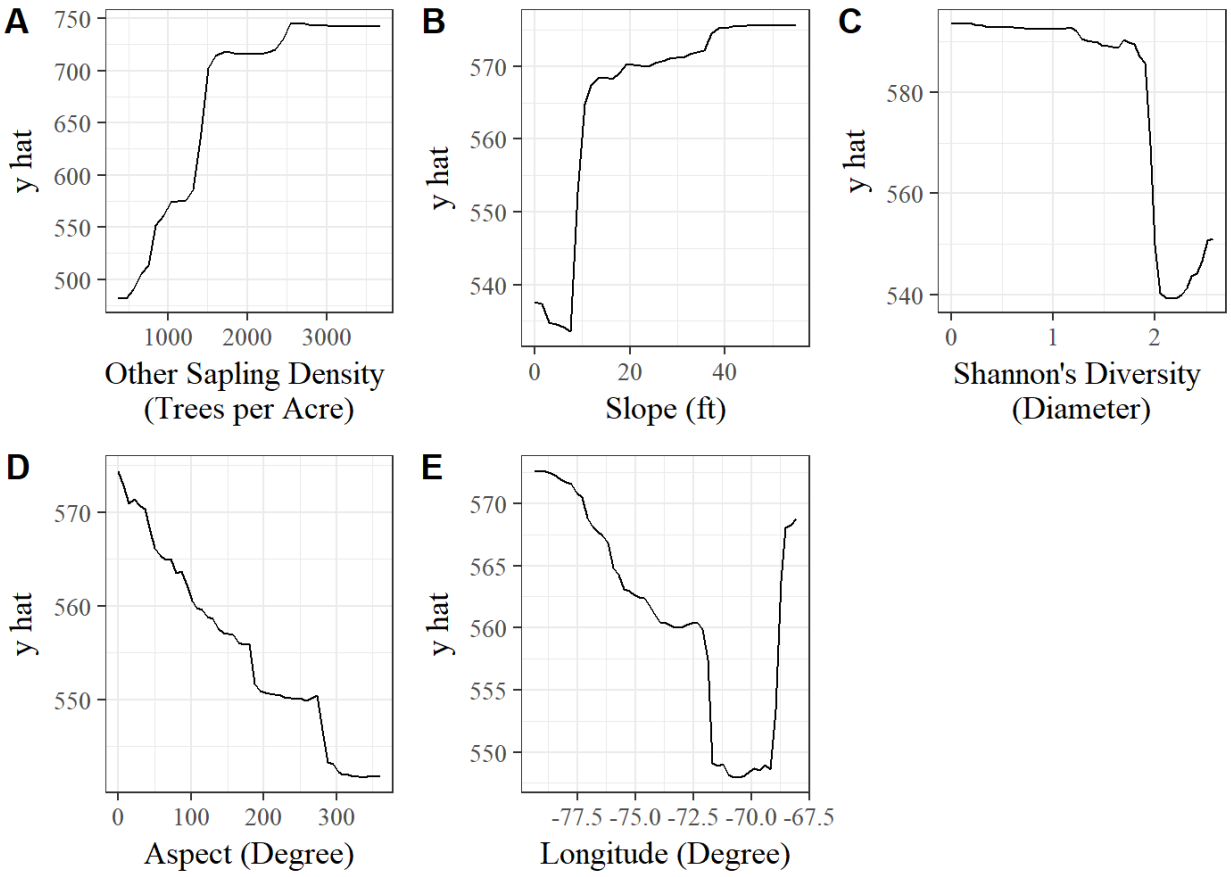

Figure 2-7. Partial dependence plots for sugar maple sapling density on all plots with adequate regeneration. Top five variables.

Tables

Table 2-1. Seedling density of sugar maple and yellow birch by litter depth with simple linear regression trend line and 95% confidence interval.

Table 1.	Variable Name	Mean	Std. Dev.	Range
Response Variables				
Sugar Maple Sapling Density (stems ha^{-1})	SM_TPA_LIVEsap	226.9	386.1	0-3703.3
Sugar Maple Seedling Density (stems ha^{-1})	SM_TPA_seed	664.9	1282.0	0-1536.6
Explanatory Variables				
Understory Structure and Composition				
American Beech Sapling Density (stems ha^{-1})	AB_TPA_LIVEsap	354.8	527.3	0-3518.1
American Beech Seedling Density (stems ha^{-1})	AB_TPA_seed	454.8	672.0	0-8656.4
Total Sapling Density (stems ha^{-1})	TPA_LIVEsap	1318.2	1179.8	0-10554.3
Total Seedling Density (stems ha^{-1})	ALL_TPA_seed	2390.9	2357.4	0-27589.5
Overstory Structure and Composition				
Sugar Maple Basal Area (m^2 ha^{-1})	SM_BA_LIVEover	9.6	6.1	0.2-40
American Beech Basal Area (m^2 ha^{-1})	AB_BA_LIVEover	2.1	3.1	0-20.7
Total Basal Area (m^2 ha^{-1})	BA_LIVEover	20.2	9.0	0.2-60.3
Shannon's Diversity Index of Species	HSpecies	1.21	0.4	0-2.4
Shannon's Diversity Index of Diameter	HDiam	2.1	0.3	0-2.8
Quadratic Mean Diameter (cm)	qmd	26.2	4.8	12.7-59.1
Total Stand Density (stems ha^{-1})	TPA_LIVEover	369.8	145.2	14.8-1159.4
Site Characteristics				
Latitude	LAT	--	--	
Longitude	LON	--	--	
Elevation (m)	ELEV	446.5	117.4	18.2-993.6
Aspect (degrees)	ASPECT	126	111.78	0-360
Slope (%)	SLOPE	17.21	12.96	0-90
Plot Location	PLOT	--	--	

Climate				
Growing Season Precipitation (cm)	GrowPRCP	93.61	57.57	0-265.9
Mean Annual Temperature (^{o}C)	monthTemp	5.87	1.69	0-12.4
Soil Characteristics				
Soil Depth (cm)	soil_Depth	119.2	21.16	0-160
Soil ph	soil_pH	4.97	0.52	0.07-7.01
Soil Available Water (cm^3)	soil_Avail	12.16	5.39	0-98
Site History				
Management (Binary, 1:Yes or 0:No)	Management	1:13% 0:87%	--	--
Disturbance (Binary, 1:Yes or 0:No)	Disturbance	1:12% 0:88%	--	--

CHAPTER 3: LONG-TERM REGENERATION DYNAMICS ACROSS A RANGE OF SILVICULTURAL INTENSITY AND SITE QUALITY IN NORTHERN HARDWOODS

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3.1 Abstract

Consideration of site conditions for selecting the appropriate silvicultural system has been central to northern hardwood management for centuries. Yet, reliance on more generalized, regional silvicultural guides has increased in recent decades resulting in inconsistent treatment outcomes with regard to forest structure, composition, and regeneration. To examine the long-term interactions between silvicultural outcomes and site, we analyzed commonly applied even and uneven-aged systems across a range of site conditions in the northeastern United States. Results from long-term measurements (20+ years) showed many different silvicultural systems can be used to maintain species and structural diversity in northern hardwood forests, but not without consideration of American beech (*Fagus grandifolia*). In the absence of persistent beech control, only sites managed with greater harvest intensities, i.e. clearcut, shelterwood, or group selection, retained sustainable amounts of sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghanesis*) in the overstory and regeneration layer.

3.2 Introduction

The influence of site conditions on the outcomes of silviculture treatments has been central to the development and refinement of silvicultural methods for centuries (Toumey et al. 1927; Puettmann et al. 2009). This has included accounting for the ecology of desired species in the context of local conditions, such as climate, soil, and wildlife population densities (Toumey et al. 1927;Spurr and Cline, 1942). Further refinement of silvicultural systems has also incorporated feedbacks between resulting stand conditions and susceptibility to abiotic factors such as wind throw and snow damage (O'Hara and Ramage, 2013). Despite the historic emphasis and tailoring of silvicultural systems to specific site conditions and regions, the past several decades have witnessed translation of these systems into broad recommendations often meant to encompass the entire range of a species or forest type (e.g., Johnson and Smith, 2009; Tubbs, 1977). Such guides are a useful tool for broad management constructs in a given forest ecosystem, but often lack the integration of site-specific considerations needed for consistent results (Kern et al., 2017). Revisiting and emphasizing potential variation in site-level silvicultural outcomes is critical for ensuring the effective application and evolution of management regimes to address current and future management objectives.

Across forest types, silvicultural treatments tailored to site-specific conditions have proven crucial for increasing productivity in managed systems (D'Amato et al., 2017), conferring resilience to the impacts of natural disturbance and non-native insects and diseases (Waring and O'Hara 2005), and for securing desirable regeneration (Larsen and Johnson, 1998). For example, silviculture incorporating fertilization, site preparation, and genetically-improved planting stock tailored to specific site requirements has resulted

in greater than 100% gains in growth relative to more general strategies historically used in pine plantations in the southeastern US (Fox et al., 2007). In the context of forests experiencing severe disease or insect outbreaks, management that incorporates site-level factors more effectively reduces pest damage (Waring and O'Hara, 2005); as seen in lodge pole pine (*Pinus contorta*) forests of western North America impacted by recent mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Han and Renzie, 2005).

Accounting for site attributes and stand conditions (i.e. advance regeneration, nutrient demands of overstory species, and species composition prior to disturbance) has also been demonstrated as a crucial factor for maintaining structural and compositional diversity over time and across the landscape in boreal and temperate forest systems (Bergeron et al., 1999; O'Hara, 1998). Site components, such as edaphic conditions (Tubbs, 1977), local populations of herbivores (Rooney and Waller, 2003), and stand level topography (Clinton et al., 1994) can also strongly influence recruitment patterns in response to a given silvicultural treatment. Yet, despite the benefits observed from the application of site-based silviculture, many regions and forest types still rely on broad recommendations developed over the past several decades.

The northern hardwood forests of northeastern North America are an example of a forest ecosystem spanning a wide variety of site types and correspondingly warranting consideration of site-specific silvicultural systems. These forests encompass well drained, rich sites of nearly pure sugar maple (*Acer saccharum*), moderately-well drained glacial tills supporting a mixture of hardwood species, and poorly drained lowlands of red maple and mixed conifers (Halliday, 1937). Despite this variety, historic

management of these forests has witnessed several phases devoted to developing and advocating for the wide application of a single, given silvicultural system (Smith, 1972).

Uneven-age systems have been widely applied since the early days of management in northern hardwood forests, due partly to their ability to promote and maintain stands dominated by economically valuable shade-tolerant species, namely sugar maple (Frothingham 1915; O'Hara, 2002). As with other forest types, an additional early justification for uneven-aged approaches, particularly single-tree selection, was a desire to generate a steady and sustainable supply of valuable wood over time, (Hawes and Chandler 1914; Eyre and Neetzel 1937; Hough and Taylor 1946). This approach was supported by guidelines developed in the mid-20th century for single-tree selection based on theoretical balanced stand conditions and early experiments with partial harvesting at the Dukes Experimental Forest in the Upper Peninsula of Michigan (Eyre and Zillgitt, 1953). Complementary research was developed in parallel at the Bartlett Experimental Forest in New Hampshire where group selection was advocated for maintaining mid-tolerant species and addressing the patchy nature of mature northern hardwood forests in the region (Gilbert and Jensen, 1958). Long-term outcomes of experiments applying these early guidelines have provided examples of improved residual stand quality and successful regeneration of desired species across the range of northern hardwood forests (Bédard et al., 2014; Kenefic and Kern, 2013; Nyland, 1998). Results have emphasized the appropriateness of single-tree selection where tolerant species and high value products were the desired outcome (Keyser and Loftis, 2013; Leak et al., 1987), while group selection offered a more flexible approach that promoted species diversity and the structural attributes associated with uneven-age management. Both forms of selection

cutting represent a lower intensity silvicultural approach relative to even-age systems, making them ideal for ecologically sensitive areas or those subject to public review (Yamasaki et al., 2014).

Although the benefits of selection systems have long been studied, limitations for these methods have also been noted. The lower reductions in basal area and subsequent reductions in canopy disturbance have resulted in an increased dominance of shade-tolerant species, particularly American beech (*Fagus grandifolia*) in the northeastern US and sugar maple in the Lake States, at the expense of desirable, less-tolerant species such as yellow birch (Ostrofsky and Mccormack, 1986, Marquis et al. 1992). In regions with elevated deer populations, regeneration following selection harvests is subject to heavy browse damage often resulting in regeneration failure in the absence of browse control measures (Kittredge et al., 1995; Marquis, 1974). From an operational perspective, the time and skill required for the application of uneven-age management via structural guidelines has proven too operationally restrictive for wide-spread use (Brockway et al., 2015).

Alternatives to uneven-age methods have been put forward, in part as response to the above concerns, but also to increase economic efficiency (Erickson et al., 1990; Nyland, 2005). The shelterwood system was proposed as one such alternative (Leffelman and Hawley 1925); however, this system has been less widely studied given the early emphasis on creating balanced uneven-aged conditions. Shelterwood methods have been applied to northern hardwood forests in regions where policy or public opinion made clearcutting an undesirable approach (Hannah, 1988; Tubbs, 1969). In the Adirondack region of New York, yellow birch and sugar maple were successfully regenerated with a

low density, uniform shelterwood following chemical control for beech and increased hunting to limit white-tailed deer (Kelty and Nyland, 1981). However, economic and operational considerations for removal of the overwood (Leak et al., 2014) as well as a high percentage of nonindustrial land owners with preference for minimal impact management has encouraged more widespread use of uneven-aged systems for northern hardwood forests (Kelty et al., 2003)

There are many economic, ecological, and social factors that can justify the use of even or uneven-age methods of management in northern hardwood forests; however, results from any method will be inconsistent if management does not consider the underlying attributes of a site that drive species composition and development (Leak, 1980; Nyland et al., 2006; Ray et al., 2008). Cross-site comparisons over long time periods have rarely been conducted to assess these inconsistencies and further refine guidance on what methods of management may be most appropriate. This knowledge is particularly important given the reliance on adequate and desirable natural regeneration to sustain northern hardwood systems over time (Brissette, 1996). In addition, as global stressors, including climate change and non-native invasive species, further impact these forests, an understanding of the influence of site conditions will be critical to informing adaptation strategies for sustaining this resource. This research takes advantage of a unique collection of long-term silviculture studies spanning a range of site types and treatments to develop a comprehensive assessment of the site-specific outcomes associated with silviculture in northern hardwood forests. The specific objectives of this research are to: 1) describe impacts of treatments on stand species composition, structure,

and diversity over time and across different site types and 2) characterize long-term effects of silvicultural systems and site conditions on regeneration of desired species.

3.3 Methods

3.3.1 Study Sites

This research utilizes long-term data from three silvicultural studies within the northern hardwood forest type in the northeast United States. Two studies, Huntington Wildlife Forest and the Forest Ecosystem Demonstration Area, are in the Adirondack region of New York. The third study location is in the White Mountains of New Hampshire at the Bartlett Experimental Forest. Broadly, climate at these locations is classified by cold winters with ample snow accumulation and temperate summers. Temperatures range from –5 to 32^{o}C and precipitation averages 1270 mm (Adams et al. 2003; Kelty and Nyland, 1981).

Huntington Wildlife Forest

Hunting Wildlife Forest (HWF) is located in Newcomb, New York in Hamilton and Essex counties. The property has been owned and managed by the State University of New York College of Environmental Science and Forestry (SUNY ESF) since 1932. Prior to ownership by SUNY ESF there was some selective cutting for red spruce on the forest (McGee et al. 1999). Soils on site are primarily in the Becket series, classified as deep, well drained loamy soils (USDA). Elevation of sites ranged from 520 – 580 m with a growing season that lasts between 100-120 days (Kiernan et al., 2009). Northern hardwoods are the dominant species throughout the forest, especially on the better drained mid-slopes (Ray et al., 1999). Reduction of the local deer population has been a

broad objective at HWF since 1966 (Kelty and Nyland, 1981). Increased hunting efforts have reduced deer densities from 70 to 31 per km^2 (Behred et al. 1970).

This work takes advantage of four silvicultural studies at HWF, three single-tree selection and one uniform shelterwood study. Treatment length varies as do specifics of past land use and beech control. Single-tree selection studies, Gooseberry Mountain (HWF GM), Junction (HWF J), and Old Military Road (HWF OMR) were established in maturing northern hardwoods in the mid- to late 1980s, each with a single entry since that time. All treatments received herbicide application to reduce beech components prior to harvest. In the Junction stand any beech remaining after harvest were treated with additional hand-held herbicide. Studies range in size from 4 to 18 ha. Single-tree selection systems were applied following the diameter guides developed by Eyre and Zillgitt (1953) and Arbogast (1957) with preference for sugar maple and yellow birch. Initial basal areas ranged from 12.1 $m^2\ ha^{-1}$ to 18.3 $m^2\ ha^{-1}$ (Table 3-1).

The fourth study from HWF is a uniform shelterwood (Wolf Lake Shelterwood [HWF WL]) established in 1968. There was an initial entry between 1968 and 1969 reducing the basal area to 13.7 $m^2\ ha^{-1}$ (Table 3-1) and the overwood was removed 10 years later (Kelty and Nyland, 1981). Prior to the establishment cut, mist blowing treatments of 2-4 D were applied to reduce the beech component.

Pre-treatment data on forest structure and composition is only available for one stand at HWF (Junction) and was used to represent the general condition of the forest prior to treatment for all areas examined. To characterize long-term structural and compositional outcomes, permanent plots, 0.08 ha and variable radius, were established at each stand in a grid fashion for repeated measurement at the onset of treatment

implementation. The most recent inventory was completed in 2016 using variable radius plots with a nested 1/20 ha plot to measure saplings 2.54 to 8.6 cm at breast height and a 1/404 ha plot to measure regeneration (seedlings to stems < 2.54 cm dbh).

Paul Smiths Forest

The Forest Ecosystem Demonstration Area (FERDA) study is located at Paul Smiths Forest (PSF) in Paul Smiths, NY in Franklin County. Elevation is approximately 520 m. Soils on site are in the Adam series, deep excessively drained sands (USDA). Prior to harvest, FERDA composition was primarily sugar maple, yellow birch and American beech with mixed conifers and some red maple (Smith et al., 2008). The study was established in 1998 as a collaboration between the U.S. Forest Service Northern Research Station and Paul Smiths College. Prior to installation of the FERDA treatments the site was dominated by maturing northern hardwoods. Prior harvesting was selective removal of valuable hardwood species (Twery personal communication). Seven replicated silvicultural systems are included in the broader FERDA study, four are included in this work, single-tree selection (FERDA STS), group selection (FERDA GS), uniform shelterwood (FERDA SW), and clearcut (FERDA CC). Each treatment is comprised of two, two-ha blocks. Initial basal areas for each treatment ranged from 33.0 $m^2 ha^{-1}$ in the single-tree selection to 23.1 $m^2 ha^{-1}$ in the shelterwood (Table 3-1). Single-tree and group selection systems were implemented using q-factors of 1.4 and 1.3 respectively, each removing approximately 30% of the tree volume on a 20-year cutting cycle (Smith et al., 2008; Twery et al. 2013). In the uniform shelterwood treatment, approximately 70% of total overwood cover was removed in the initial harvest to promote establishment of a single-age stand. A second entry in the shelterwood treatment

occurred in 2014 to remove remaining overstory trees. All trees were removed during the clearcut to favor regeneration of more shade-intolerant species. Prescribed residual basal areas for each treatment were between 0 m^2ha^{-1} in the clearcut and 14.6 m^2ha^{-1} in the single-tree selection.

Eight circular fixed area plots (0.04 ha) were established in each treatment block for repeated measurements of trees ≥ 2.5 cm at breast height with measurements occurring pre and post-treatment in 1998. A follow-up inventory was conducted in 2014.

Bartlett Experimental Forest

The Bartlett Experimental Forest (BEF) has been owned and managed by the U.S. Forest Service Northern Research Station since 1932 (Leak and Yamasaki, 2011). This Experimental Forest is in the White Mountains of New Hampshire in the town of Bartlett, located in Carroll County. Land use history of the BEF prior to management by the USFS is not well documented, although the northern portion of the forest may have been used over a short period for agriculture in the late 1700s or early 1800s (Leak and Yamasksi 2001). The higher elevation portions of the forest were also likely selectively cut for softwoods, including some removal of hemlock for tanning (Leak and Yamasaki 2011). Elevation on the forest ranges from 200 m to 900 m with rocky outcroppings increasing at higher elevations. Soil composition is variable, but generally derived from granite and schists of glacial origin. Soils are sandy loams, Berkshire, Marlow, and Marlow-Peru soil series (Sendak et al., 2000).

This research utilized seven, unreplicated silvicultural treatments from the long-term Compartment Management Study. Treatments represent a gradient of management intensities from clearcut to single-tree selection. As part of the study 48 experimental

units were established, with seven units included in this work. At the time of study establishment, stands were irregular, uneven-age northern hardwoods. Beech and red maple are dominant species throughout the BEF, although sugar maple, yellow birch, other hardwoods and softwoods are also present (Sendak et al. 2000). Three single-tree selection stands were included, (BEF C42, BEF C43, and BEF C46), each established in the early 1950s (Table 3-1). Single-tree selection stands were initially attempted using a Q factor of 1.5. Compartment 42 has received three cuts, first in 1952, then again in 1975 and 1992. Compartments 43 and 46 were first cut in 1957, and again in 1998-1999. Three group selection stands were also used for this work, BEF C5, CBEF6, and BEF C31). Outcomes for BEF C5 and C6 are combined for this work given spatial proximity of these two units (Hereafter referred to as "C5&6"). Groups were established using area control targeting removal of pockets of mature trees or release of areas of desirable advance regeneration (Leak Personal Communication). C 5&6 has received four entries since 1937. Compartment 31 was first cut in the early 1950s then again in the early 1960s, most recently in 1998-1999 (Yamaski and Leak 2004). Compartment 35 was originally treated with single-tree selection, but later converted to a shelterwood system in 1999 leaving 7.3 m^2ha^{-1} of basal area as overwood (Yamaski and Leak).

Trees greater than 5 cm were measured using square 0.1 ha plots established on a grid across the entire BEF for all plots and inventories excluding the 2017 inventory of Compartments 5 and 6. Most recent inventories for all other compartments occurred between 2001 and 2003. Data from C 5&6 were measured using variable radius plots with nested circular 0.08 ha fixed area plots. For all studies, initial inventories and the most recent inventories were used to compare pre and post treatment conditions.

3.3.2 Analysis

To address the variability across inventories and shifts in data collection over time, variables included in analysis were restricted to those consistently measured across sites or that could be consistently calculated from available data. As such, this work focused on metrics from live trees only. To quantify the evolution of stands over time, measures of species composition, forest structure, diversity, and regeneration dynamics were calculated for pre-treatment data and current inventories. Modeling work was also used to evaluate influential factors for regeneration success. Overstory trees were classified by a dbh ≥ 11.5 cm, saplings size classes were individuals between 5 and 11.4 cm dbh.

Overstory Composition and Structure

Overstory composition and structure was evaluated using readily available metrics to capture the general transition of stands with time and treatment. Shifts or changes in species for a given stand was measured using species importance values, IV. Species importance values weight the total number of stems and volume of a given species or species group, IV and was calculated as:

[1] $$IV = (RDen + RDom)/2$$

Where RDen is the relative density in trees per hectare and RDom is the relative dominance in basal area per hectare by species group. Species groups considered for this analysis were American beech, sugar maple, yellow birch, other hardwoods, and softwoods. Considered species or groups capture desirable species for the region (sugar maple and yellow birch), economically undesirable species (American beech), and variability attributable to management, site, and additional factors (other hardwoods and

softwoods). Change in species importance values over time were measured by percent change in IV between the initial and final inventories.

In addition to the overall importance of any one species or group in a stand, Shannon's diversity index, HSpecies, was used to assess the complexity of species composition. Higher values of H signal greater species diversity (more species in total), lower values signal less diversity (Staudhammer and LeMay 2001). For this analysis HSpecies was calculated using the Vegan package in R (https://cran.r-project.org/).

Stand structure was evaluated using total tree density (trees ha^{-1}), volume in basal area ($m^2\,ha^{-1}$) and diversity of diameter distributions, HDiam. Greater values of HDiam show stands with a greater number of overstory diameter classes while lower values show a narrower range of diameter classes. HDiam was also calculated using the Vegan package in R. For uneven-age treatments, plotted diameter distributions were created as a further evaluation of stand structure. Diameter distributions were classified into different forms using the methods of Janowiak et al. (2008), with reverse J, rotated sigmoid, concave, increasing q, unimodal, and variable used as potential classifications.

Regeneration Dynamics

In addition to the overstory conditions over time, we also assessed regeneration dynamics using density of established regeneration, stocking, and species composition as a function of density. Regeneration calculations were completed for the same species and species groups as described above. Regeneration success was measured via density and stocking of desired species (sugar maple and yellow birch) relative to previously established regional guidelines (Leak et al., 1987; Marquis et al., 1990; Tubbs, 1977).

Calculated values of regeneration were further supplemented with three recruitment models. Models emphasized desired species with a separate model for sugar maple and yellow birch and final model with these two species combined. Model form and included variables were based on data and characteristics available for each site and stand. Additionally, models relied on existing ecological knowledge. Regeneration inventories were highly zero inflated, a common occurrence in recruitment data (Li et al., 2011), leading to a zero-inflated modeling approach. The negative-binomial form was chosen as data were counts where variance did not equal the mean. The resulting model forms were mixed effects, zero-inflated, and negative binomial as seen below:

[2] $SM = Plot{:}Stand{:}Forest + HDiam + HSpecies + treatment + time + \in$

[3] $YB = Plot{:}Stand{:}Forest + HDiam + HSpecies + treatment + time + \in$

[4] $YB + SM = Plot{:}Stand{:}Forest + HDiam + HSpecies + treatment + time + \in$

Random effects in the model are plot, nested in stand, nested in forest. Fixed effects in the model are HDiam, HSpecies, treatment (the silvicultural treatment), and time (year since treatment initiation). SM and YB are sapling density of sugar maple and yellow birch, respectively. After the initial run for each model, variables not significant at an alpha 0.05 were removed and the models were re-run until all fixed effects were significant. The final model forms were,

[5] $SM = Plot{:}Stand{:}Forest + treatment + time + \in$

[6] $YB = Plot{:}Stand{:}Forest + HDiam + HSpecies + time + \in$

[7] $YB + SM = Plot{:}Stand{:}Forest + HDiam + time + \in$

Full and reduced models were compared by change in AIC. Model performance was assessed by the squared correlation between model predicted values and observed regeneration values.

3.4 Results

3.4.1 Overstory Dynamics

American beech remained a viable species in all even-age stands following harvests with sugar maple IV comparable to beech in shelterwood stands and yellow birch IV exceeding beech in the FERDA clearcut (Figure 3-2). Percent change in beech was negative for all even-age stands over time (Figure 3-2). Change in sugar maple and yellow birch over time was less consistent across even-age treatments. Sugar maple percent change was positive, albeit marginally, at the HWF Wolf Lake shelterwood and BEF C35 shelterwood (Figure 3-2). In the group selection treatments beech remained a dominant species, but percent change over time was negative or minimally positive (Figure 3-3). Sugar maple and yellow birch had primarily negative percent change over time, although both species remained important species in the overstory (Figure 3). For all single-tree selection sites, beech was a dominant species in the overstory and increased over time with the exception of C46 at the BEF (Figure 3-4). Highest importance of sugar maple was following single-tree selection at FERDA, with single-tree selection stands at HWF also containing high values (Figure 3-4). The highest importance of yellow birch was in the FERDA clearcut followed by the HWF shelterwood treatment (Figure 3-2).

Trends in HSpecies values were more closely related to site than treatment and ranged from 0.48 to 2.49 (Table 3-2). Highest values of HSpecies were seen at BEF across treatments, whereas lower values were associated with HWF. Species diversity at FERDA was most variable presumably reflecting the range of applied silvicultural treatments.

Basal area and stand density decreased across all even-age systems with time (Table 3-1) ranging from 1.7 to 21.6 m^2ha^{-1} and 126.6 to 713.5 stems ha^{-1}, respectively. In uneven-age stands, response in basal area post-treatment was variable, falling between 20.8 and 33.1 m^2ha^{-1}. At the BEF basal area and stand density increased with time, these values decreased slightly at FERDA and HWF.

For all uneven-age treatments the maximum diameters increased over time. All post-treatment diameters distributions for uneven-age stands generally had descending monotonic forms (Figure 3-5 and Figure 3-6) with classification including negative exponential, concave, rotated sigmoid, and variable distributions (Table 3-5).

3.4.2 Regeneration Dynamics

Regeneration density varied by species across sites and treatments. Beech was the most abundant species across all stands prior to harvest, and remained a dominant species by density following uneven-age treatments (Figures 3-7 to 3-9). Overall regeneration density decreased following treatments in both the FERDA and BEF shelterwoods (Figure 3-7). Density of yellow birch increased over time in the FERDA clearcut and one of the BEF group selection treatments (Compartment 5&6), but decreased in all other treatments (Figure 3-7 and Figure 3-8). Sugar maple density was

variable by treatment and site, but remained a dominant species at HWF, excluding one single-tree selection treatment (OMR) (Figure 3-7, Figure 3-9).

All sites began with beech stocking at or above 80% (Figure 3-10 to 3-12). Over time, all uneven-age treatments maintained high beech stocking relative to other species (Figure 3-11, Figure 3-12). In even-age stands, beech stocking decreased following shelterwood cutting at the BEF and FERDA (Figure 3-10). Beech stocking was comparable to sugar maple stocking in the BEF shelterwood and the HWF shelterwood (Figure 3-10). Yellow birch stocking was highest following even-age treatments, and sugar maple stocking was above 50% for all single-tree selection treatments but the OMR at HWF (Figure 3-11, Figure 3-12).

3.4.3 Regeneration Models

Outputs from regeneration models shed further light on dynamics of sugar maple and yellow birch establishment and growth. All treatment effects were negative for the sugar maple regeneration model and the model for combined sugar maple and yellow birch (Table 3-5). The effect of time was positive for both models. For yellow birch, HDiam negatively impacted regeneration, while effects of HSpecies and time were positive.

3.5 Discussion

The northern hardwood forests of the northeast United States are ecologically complex, encompassing a wide gradient of biotic and abiotic conditions. Yet, similar silvicultural systems are often applied across a range of sites anticipating consistent structural and compositional outcomes. This work offers unique insight into cross-site

evolution of northern hardwood stands under commonly applied even and uneven-age silvicultural treatments, particularly in the context of increasing beech dominance in many portions of this region (Bose et al. 2017).

3.5.1 Overstory Evolution

Across sites, overstory structural and compositional conditions reflect those anticipated for even and uneven-age silvicultural systems, specifically with regard to species diversity and structural attributes. Nearly all treatments decreased in species diversity over time (Table 3-2), but even-age treatments maintained a mixture of species in the overstory with comparable IV (Figure3-3). Retention of species diversity, specifically inclusion of more intolerant and mid-tolerant species, is frequently an objective of more intensive management i.e. clearcuts and shelterwood systems (Kochenderfer et al., 2004; Niese and Strong, 1992). Expected compositional outcomes are similar for group selection treatments, particularly those with larger gap sizes that support a greater mix of species (Lhotka, 2013; Murphy et al., 1993). Sites managed with group selection for this work had inconstant responses in IV over time (Figure 3-4). Outcomes could reflect the differences in opening size between and within treatments. At the BEF for example, initial openings were on average 0.2 ha in size, but that value increased over time to an average of 0.3 ha, with some gaps above 0.9 ha (Leak, 1999). Although group selection increases canopy disturbance relative to single-tree selection, openings below a minimum threshold will not increase recruitment of mid and intolerant species (Webster and Lorimer, 2005).

Single-tree selection treatments favoring more shade tolerant species is intentional in northern hardwoods (Jones et al., 2009; Nyland, 1998) and this outcome was observed in stands included in this analysis. Lower levels of canopy disturbance associated with single-tree selection limit survival of mid and intolerant species (Webster and Jensen, 2007), but heavily favor growth of shade tolerant species present as advance regeneration, saplings, and small sawtimber size classes (Jones et al., 2009; Lamson and Smith, 1991). An important caveat of these compositional goals is the assumption that shade tolerant species favored are economical and ecologically desirable, with sugar maple being the primary focus in northern hardwood forests. On sites in this analysis, the most shade tolerant species was American beech. Over time, the increased prevalence of beech in these stands likely will limit economic gains and ecological resilience at the expense of sugar maple and other species (Niese and Strong, 1992; Runkle, 2007; Webster et al., 2018).

Composition trends across sites and treatments were compounded by differences in time since initial harvest and harvest intensity. For example, the high proportion of yellow birch and other hardwoods in the FERDA clearcut relative to shelterwood treatments at FERDA and other sites may be attributed to the initially heavier reductions in volume (Figure 3-2), with total removal of trees in the overstory subsequently favoring a larger spectrum of shade tolerances (Hannerz and Hånell, 1997). The FERDA treatments were also cut most recently. Variability in time since harvest may emerge as compositional differences associated with changes in species dominance as stands age and mature (Gilliam et al., 1995; Leak et al., 2006).

Similar to composition, patterns in stand structure were a combination of outcomes expected for silvicultural systems as well as influences from site and harvesting attributes. Reduction in stand density and volume following even-age systems was anticipated (Smith 1997). Evolution in stand structure following uneven-age systems warranted more review. Structural guidelines were followed during establishment of all uneven-age treatments at all sites, although the rigidity and complexity of guidelines varied (Arbogast Jr, 1957; Guldin, 1991; Leak et al., 1987). Classification of diameter distributions similarly varied across sites (Table 3-5), although this variability was anticipated and has been similarly documented for other northern hardwood stands (Janowiak et al., 2008; Keyser and Loftis, 2013; Leak, 1996). Only three stands, BEF 5&6, 42, and 43 had true negative exponential curves. Both FERDA stands, the most recently harvested, were classified as concave indicating deficits in the smaller size classes (Janowiak et al., 2008). Ultimately, the variability in diameter distributions is similar to results seen in other northern hardwood forests where strict adherence to the negative exponential shape is rare and not necessarily better than other common distribution forms (O'Hara, 1998; Sendak et al., 2000).

3.5.2 Regeneration Outcomes

Regeneration across treatments and sites was prolific (Figures 3-7 to 3-9). This finding is important as nearly all silvicultural systems in the northeast rely on abundant natural regeneration (Brissette, 1996). Density and stocking of total regeneration across treatments and sites met or exceeded recommendations from regional guides (Leak et al., 2014; Tubbs, 1977) suggesting sustainable growth of northern hardwood forests through

the future. However, regeneration success is not simply measured by the total number of stems, but also distribution of commercially and ecologically valuable species (Grisez and Peace, 1973; Miller and Kochenderfer, 1998). Similar to overstory results, species response in the regeneration layer varied by silvicultural system and site. Density of yellow birch increased on two of the four even-age systems and in C5&6 at the BEF (Figure 3-7 and Figure 3-8). Other studies in northern hardwoods have observed similar increases in mid-tolerant species along a gradient of light availability (Beaudet and Messier, 1998; Gasser et al., 2010). Prior to treatment, yellow birch was marginally higher at the BEF than other sites (Figure 3-7, 3-8, 3-9), likely a result of parent material and underlying soil properties that support establishment of this species (Archambault et al., 1998; Post et al., 1969; Shields et al., 2007). Although the yellow birch regeneration model did not include treatment, negative HDiam and positive HSpecies values may indirectly represent treatments (Table 1, Table 5). Lower diameter diversity, associated with more intensive treatments and greater canopy disturbance, were also associated with higher species diversity, including yellow birch (Poznanovic et al., 2013; Raymond et al., 2003).

Trends in sugar maple regeneration were also explained by regeneration models, specifically the reductions in density of this species over time (Figure 3-7 to 3-9, Table 3-5). Stocking of sugar maple decreased following most treatments (Figure 3-10 to 3-12). Changes could reveal management actions, inherit site conditions, and their interactions that exacerbate sugar maple regeneration issues. Sugar maple is a site sensitive species, and in part establishment and growth of regeneration is limited by nutrient availability and soil moisture (Horsley et al., 2000). Recent findings from the Lake States also

demonstrate decline of regeneration is the interaction of many factors acting across scales, including deer browse, silvicultural systems, and cover of non-tree vegetation (Matonis et al., 2011). We did not measure all influential variables directly, but the negative effect of treatments in our models could partially capture them (Table 5). Competition between beech and sugar maple for available microsites may also be important (Beaudet et al., 1999), especially at sites where sugar maple increased (Junction and FERDA), as beech density also increased in these areas suggesting potential future challenges to sustaining sugar maple in these areas.

The greatest abundance of sugar maple was at HWF, soils there are finer textured and better in quality relative to other studies. HWF, although regarded as a good site in this work, is still not an enriched northern hardwood site (MSF, 2013; Thompson et al. 2000), as such, sugar maple was not competitive as advance regeneration (Nyland, 1999). Similar results have been seen in hardwood forests exposed to acid rain and subsequent nutrient depletion (Halman et al., 2015). Over time, eroding site quality lead to loss of sugar maple and favoring of American beech (Pontius et al., 2016). Recognition of these baseline predispositions is important for selecting silvicultural systems that complement rather than compete with a given site's natural dynamics (Leak, 1980).

3.5.3 Beech Management

A key finding from this work is the pervasive nature of American beech across the range of northern hardwood forests in the northeast. Since the arrival of beech bark disease, many forests in the region have experienced a shift in composition towards this shade tolerant species (Bose et al., 2017; Forrester et al., 2016; Twery and Patterson

1984) and changes in forest structure with mature trees replaced by beech sapling thickets (Cale et al., 2013; Giencke et al., 2014). The degree to which these changes occur is a function of silvicultural treatment and site conditions (Bedard and Majcen, 2001; Jones et al., 1989). As demonstrated by these findings, beech can increase in importance on poor to moderate sites and under nearly all applied silvicultural systems. If chemical beech control is part of the management strategy, sugar maple can remain competitive (Olson and Wagner, 2010; Ostrofsky and Mccormack, 1986); however, this advantage will decrease over time without ongoing application (Kochenderfer et al., 2004; Nyland et al., 2006). At HWF, a moderate site, sugar maple remains a semi-dominant species in the overstory, but regeneration is limited relative to American beech. (Figure 2, Figure 6). Beech control after the first harvest would have given sugar maple an advantage, but thirty years post-application this advantage has declined as regeneration of desired species has diminished. Single-tree selection treatments at HWF have also only seen one entry. Without further management and consistent beech control, importance of beech is likely to increase at the expense of sugar maple and other more commercially valuable species (Bohn and Nyland, 2003). Shelterwood treatments at HWF with similar beech control (Kelty and Nyland, 1981) resulted in greater levels of sugar maple to single-tree selection treatments in the same area. Similar conclusions have been reached in other forest-types with a beech component (Hein and Dhôte, 2006), particularly; as site quality decreases, more intensive management is often the only approach for maintaining species diversity and composition of desired species.

3.6 Conclusions

Regional silviculture guides provide a general framework for managing forest ecosystems at a broad scale. In forests such as the northern hardwoods, however, wide spread variability of local biotic and abiotic factors, requires silvicultural systems adjusted to specific site conditions to ensure consistent and desired outcomes. This work analyzed long-term silvicultural studies within the range of northeastern hardwood forests and found management outcomes could be attained under even and uneven-age systems. But these outcomes must be considered in the context of increasing beech dominance across the region, particularly if maintenance of sugar maple dominance and a significant yellow birch component is a long-term goal. Without direct control of beech, less intensive silvicultural treatments, especially single-tree selection, failed to maintain sustainable levels of sugar maple and yellow birch. Ultimately, on poor to moderate sites greater canopy disturbance is needed to promote composition of desired species and maintain ecosystem health and function. Traditional and evolving silvicultural methods, including clearcuts with and without retention, uniform and irregular shelterwood systems, and group selection offer viable management options moving forward.

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Figures

Figure 3-1. Location of study sites, Bartlett Experimental Forest in Bartlett New Hampshire, Forest Ecosystem Research Demonstration Area in Paul Smiths, New York, and Huntington Wildlife Forest in Newcomb, New York.

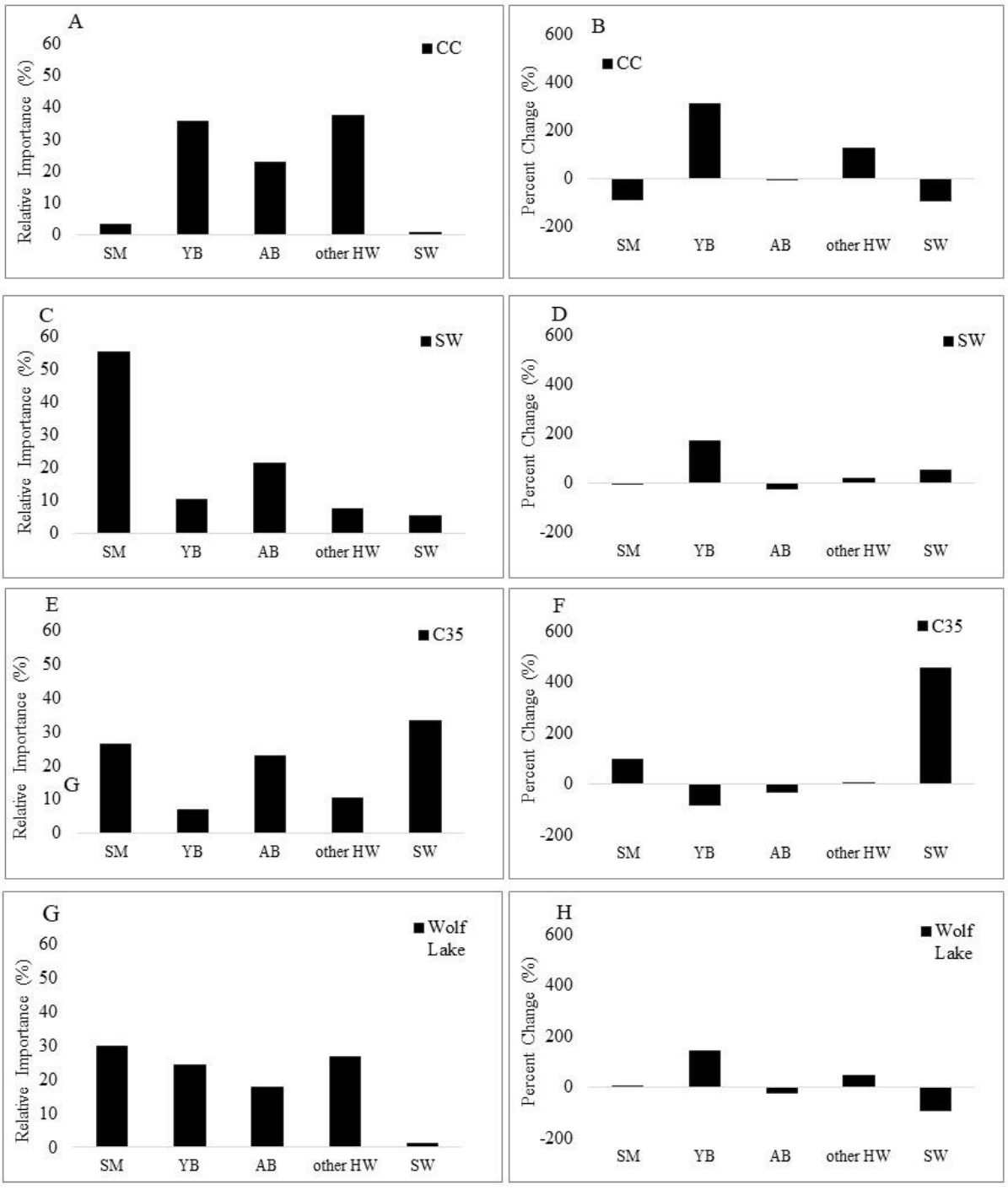

Figure 3-2. Overstory species importance values and percent change of importance values for even-age treatments. A, C, D, and G are post-treatment importance values, B, D, E, and H are percent change between initial and final inventories. Values are presented for individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA clearcut, C and D: FERDA shelterwood, E and F: BEF shelterwood.

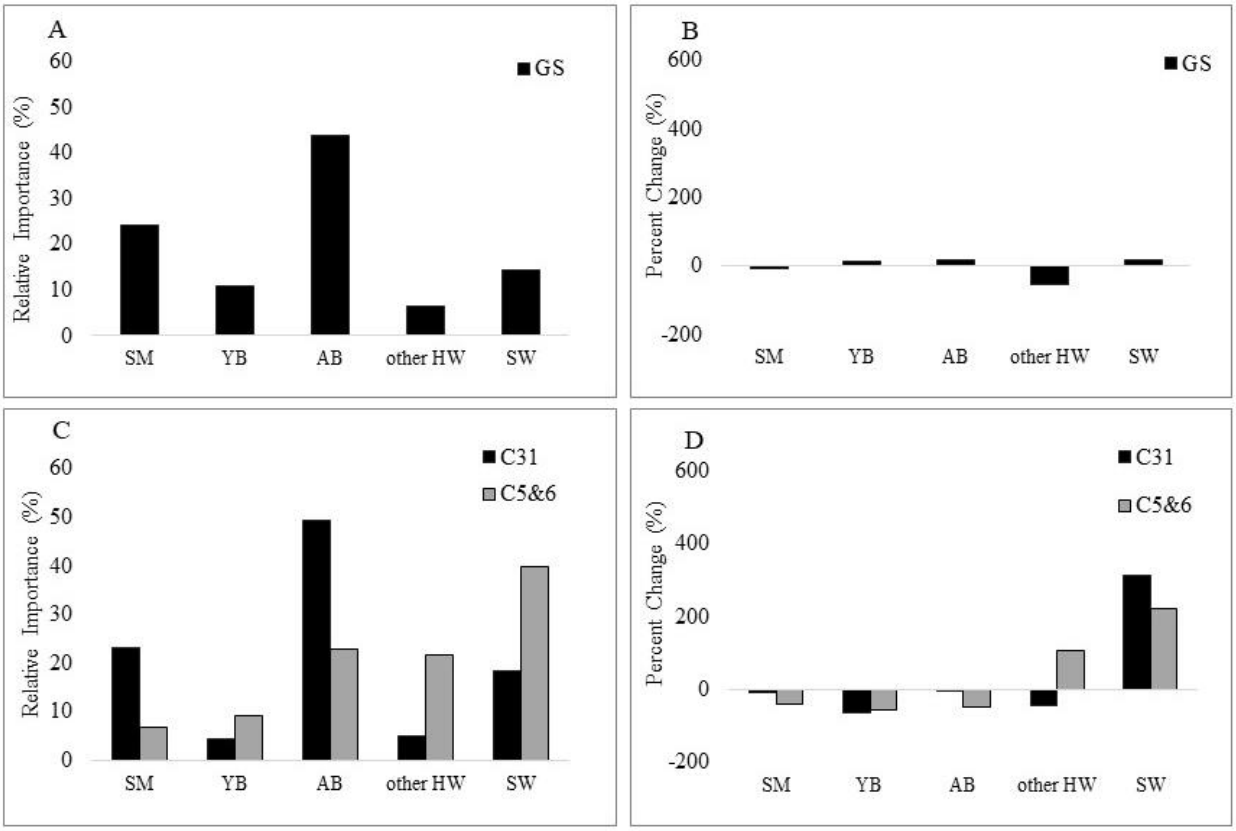

Figure 3-3. Overstory species importance values and percent change of importance values for group selection treatments. A and C post-treatment importance values, B and D are percent change between initial and final inventories. Values are presented for individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA clearcut, C and D: FERDA shelterwood, E and F: BEF shelterwood

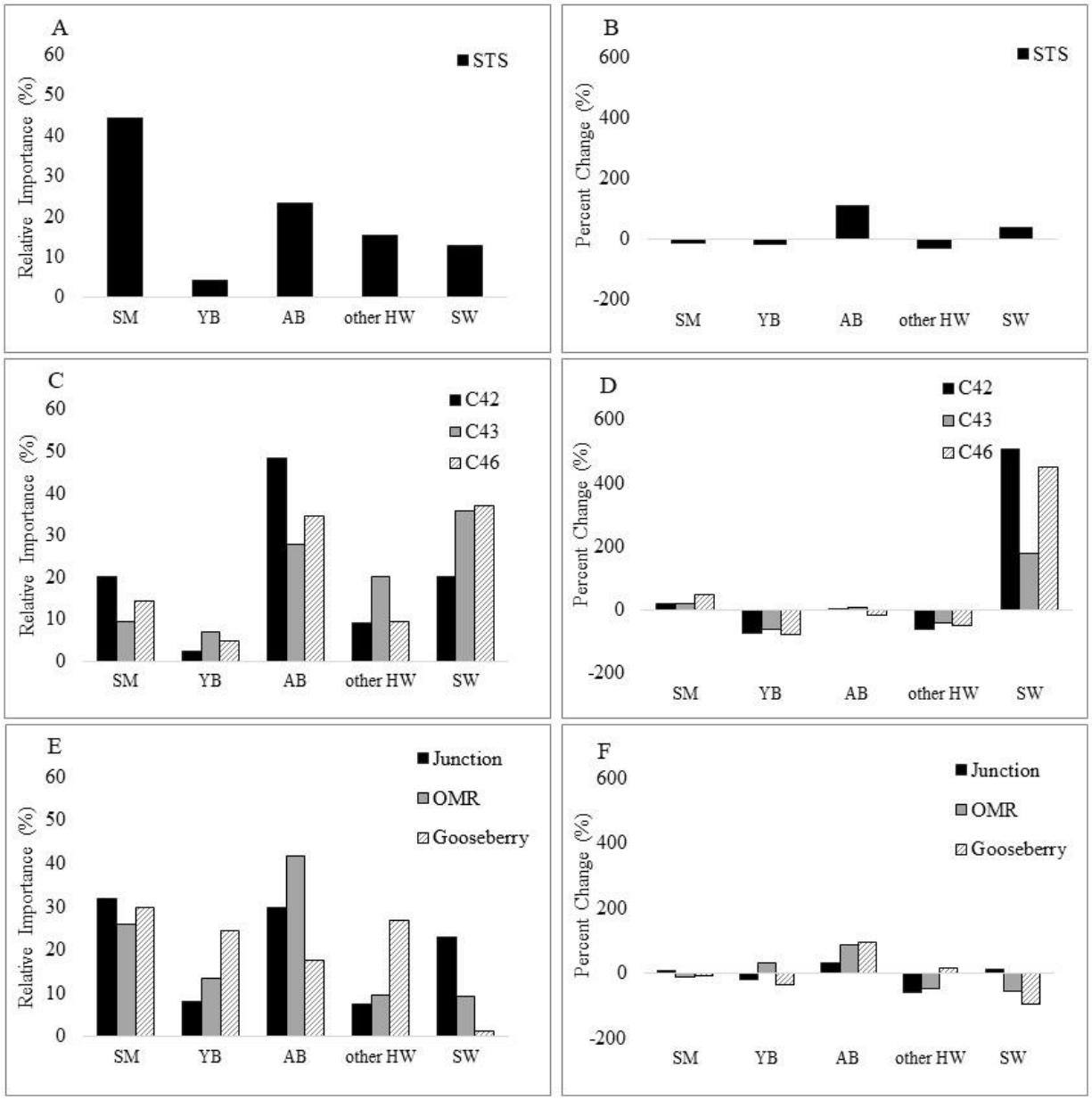

Figure 3-4. Overstory species importance values and percent change of importance values for single-tree selection treatments. A, C, and D are post-treatment importance values, B, D, and E are percent change between initial and final inventories. Values are presented for individual species or species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA clearcut, C and D: FERDA shelterwood, E and F: BEF shelterwood.

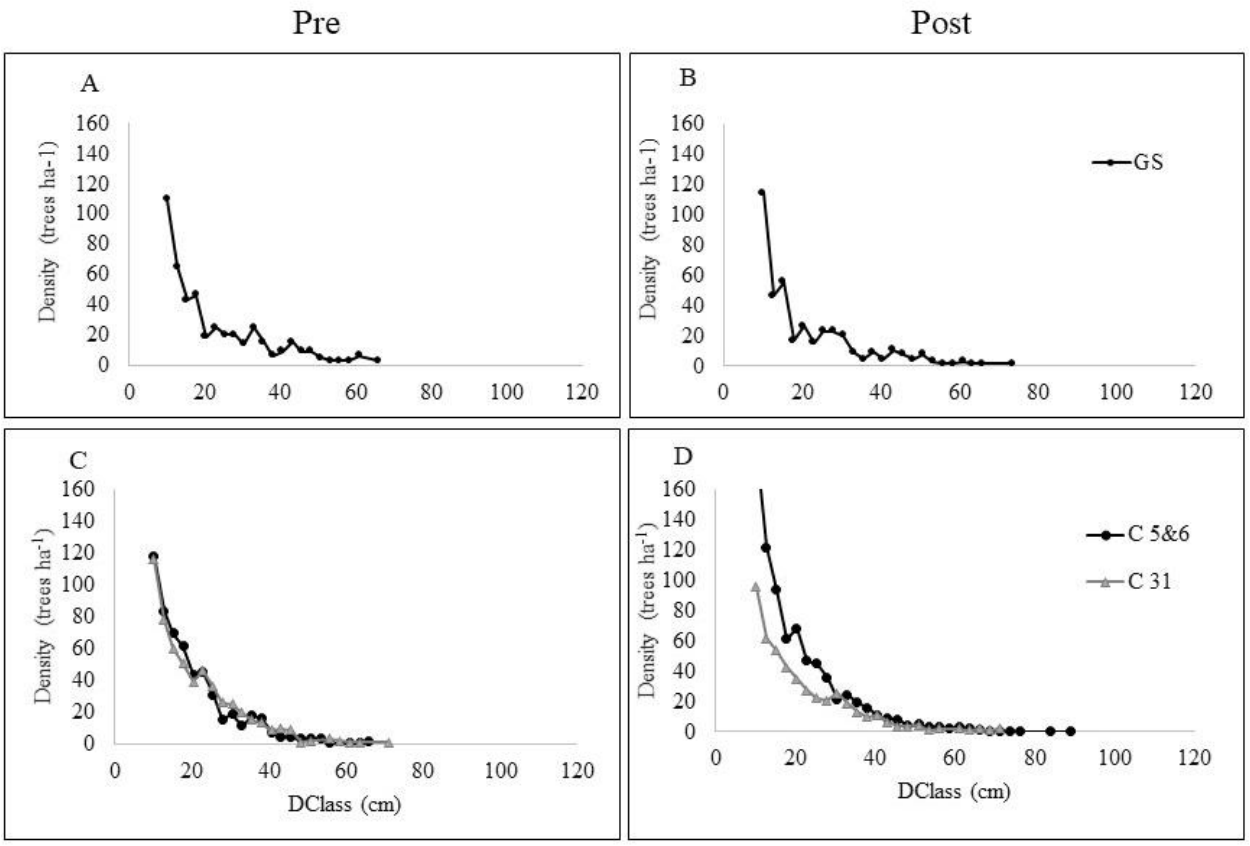

Figure 3-5. Overstory stand structure for group selection treatments by forest for pre- and post-harvest inventories. Structure is represented by density (trees ha-1) across 5 cm diameter classes. A and B: FERDA, C and D: Bartlett Experimental Forest.

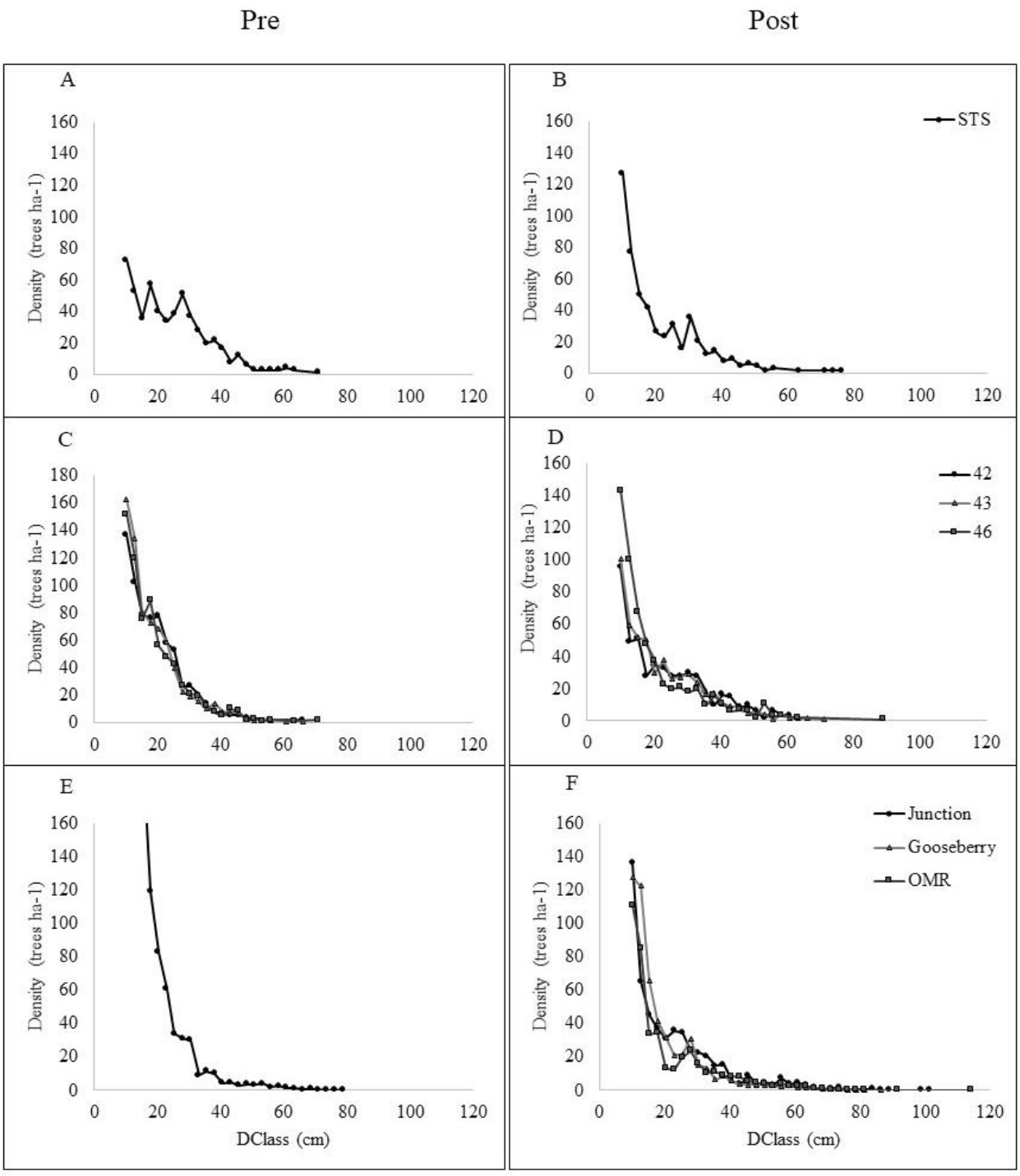

Figure 3-6. Overstory stand structure for single-tree selection treatments by forest for pre- and post-harvest inventories. Structure is represented by density (trees ha-1) across 5 cm diameter classes. A and B: FERDA, C and D: Bartlett Experimental Forest, E and F: Huntington Wildlife Forest.

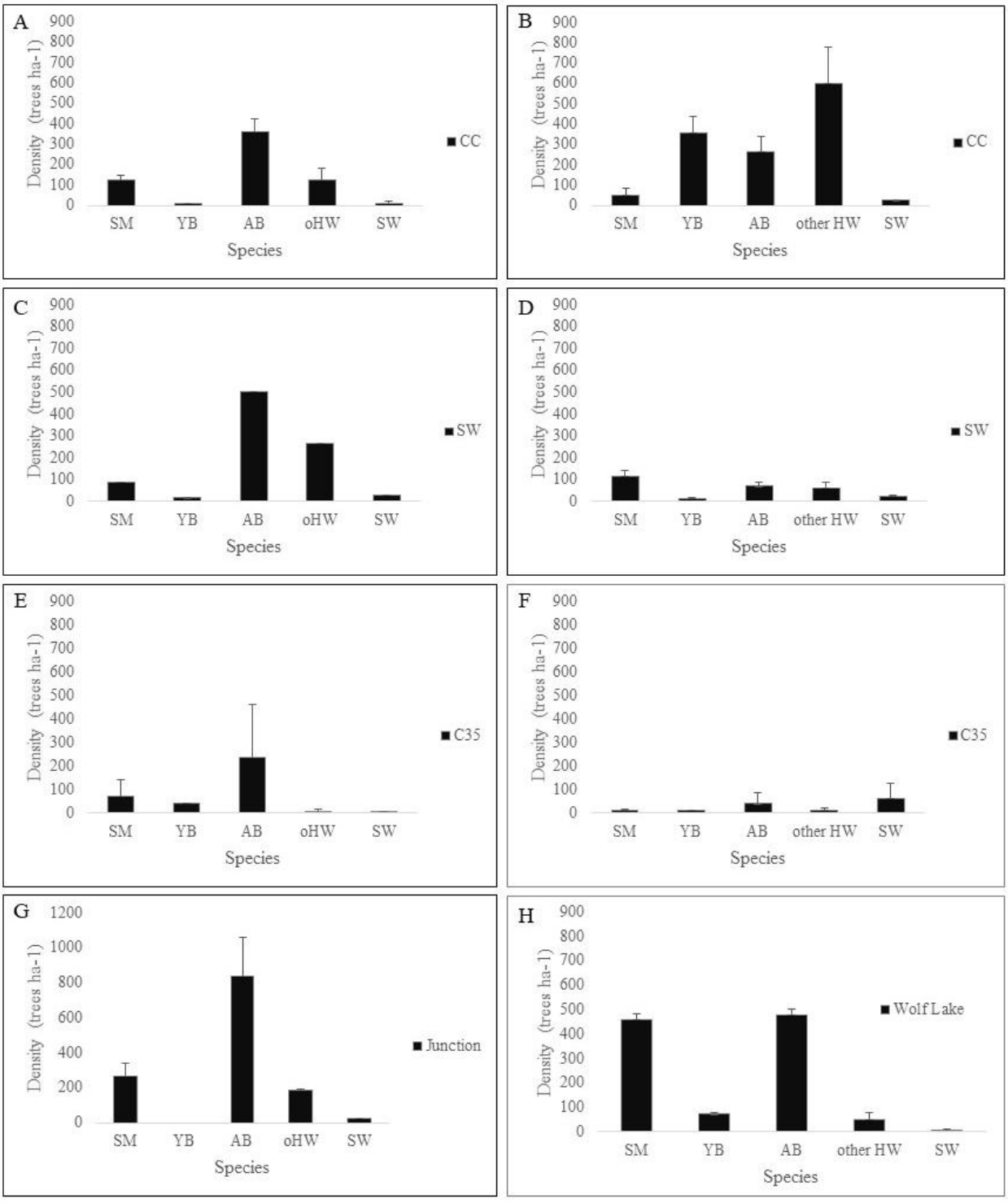

Figure 3-7. Regeneration density (trees ha-1) for even-age treatments by forest for pre- and post-harvest inventories. Densities are for individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species species), and SW (softwood species). A and B: FERDA clearcut, C and D: FERDA shelterwood, E and F: BEF shelterwood, G and H: HWF base condition and shelterwood.

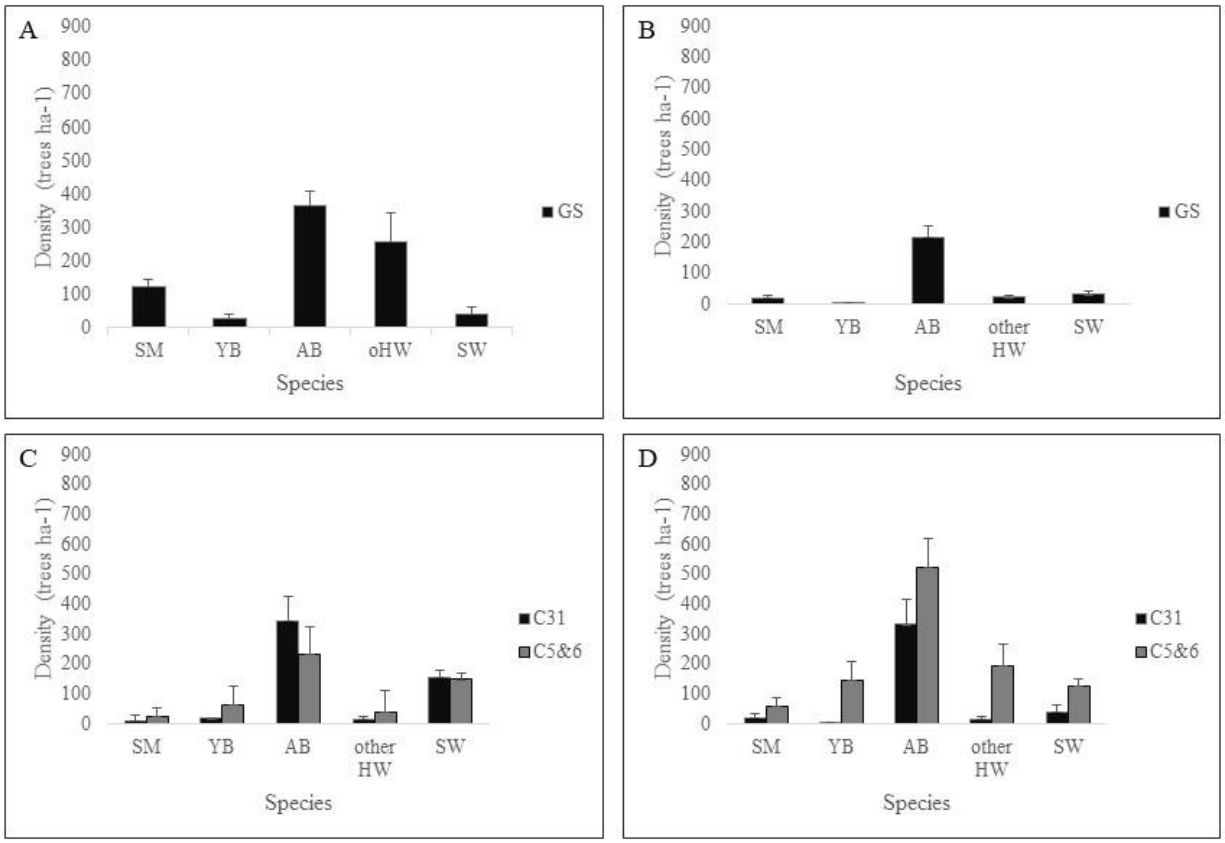

Figure 3-8. Regeneration density (trees ha-1) for group selection treatments by forest for pre- and post-harvest inventories. Densities are for individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA, C and D: BEF.

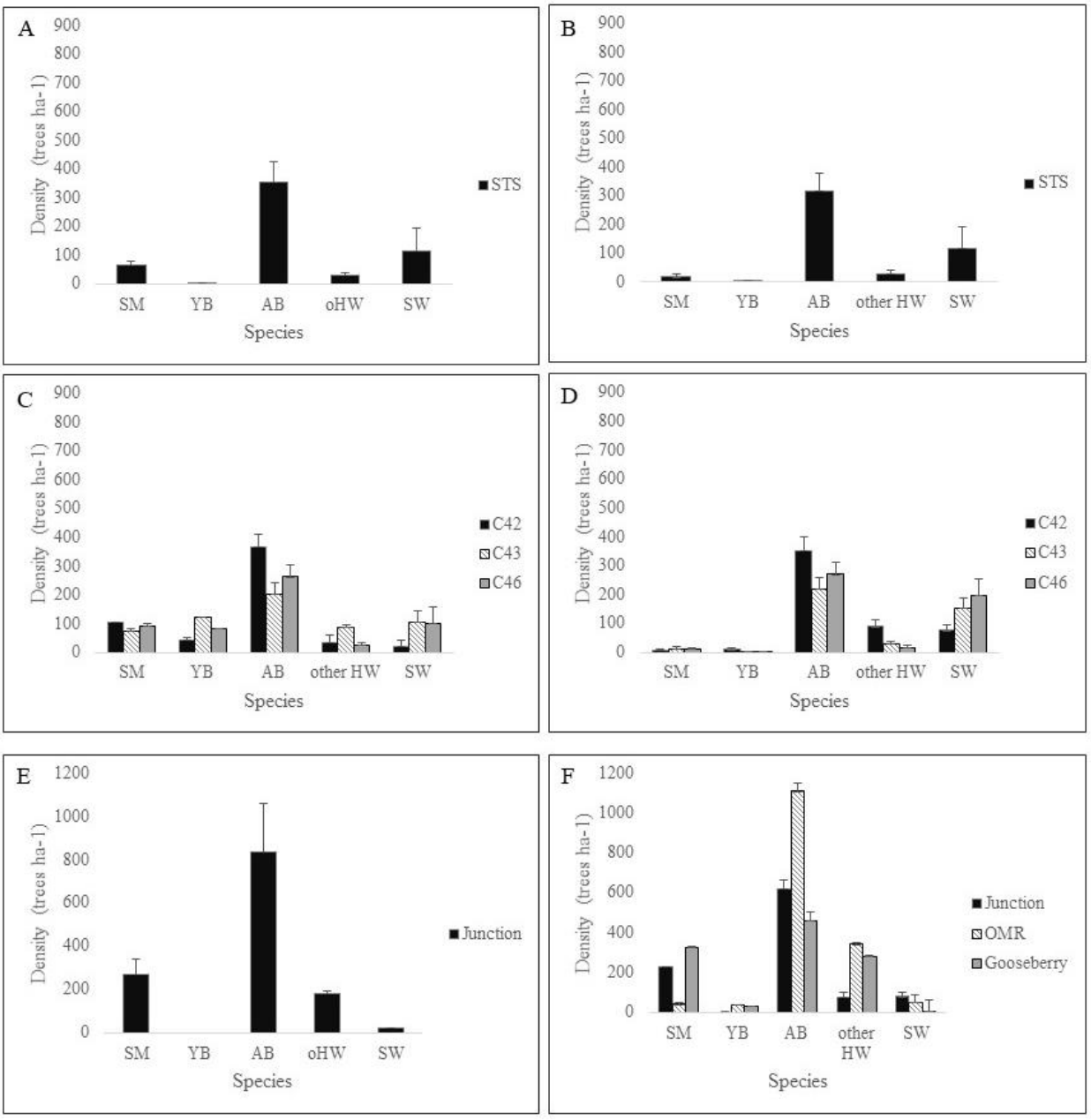

Figure 3-9. Regeneration density (trees ha-1) for single-tree selection treatments by forest for pre- and post-harvest inventories. Densities are for individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA, C and D: BEF, E and F: HWF.

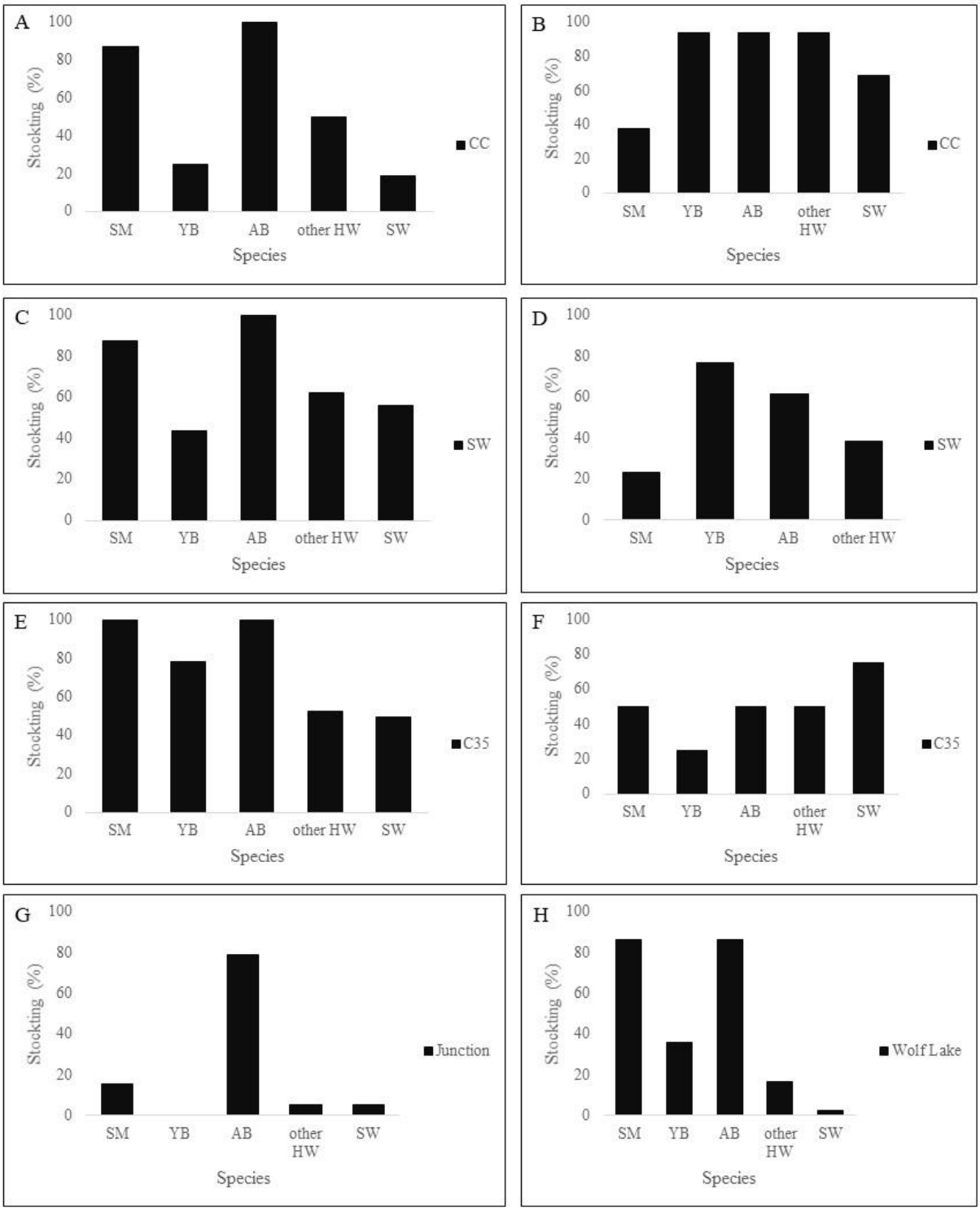

Figure 3-10. Regeneration stocking (%) for even-age treatments by forest for pre- and post-harvest inventories. Stocking presented by individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA clearcut, C and D: FERDA shelterwood, E and F: BEF shelterwood, G and H: HWF base condition and shelterwood.

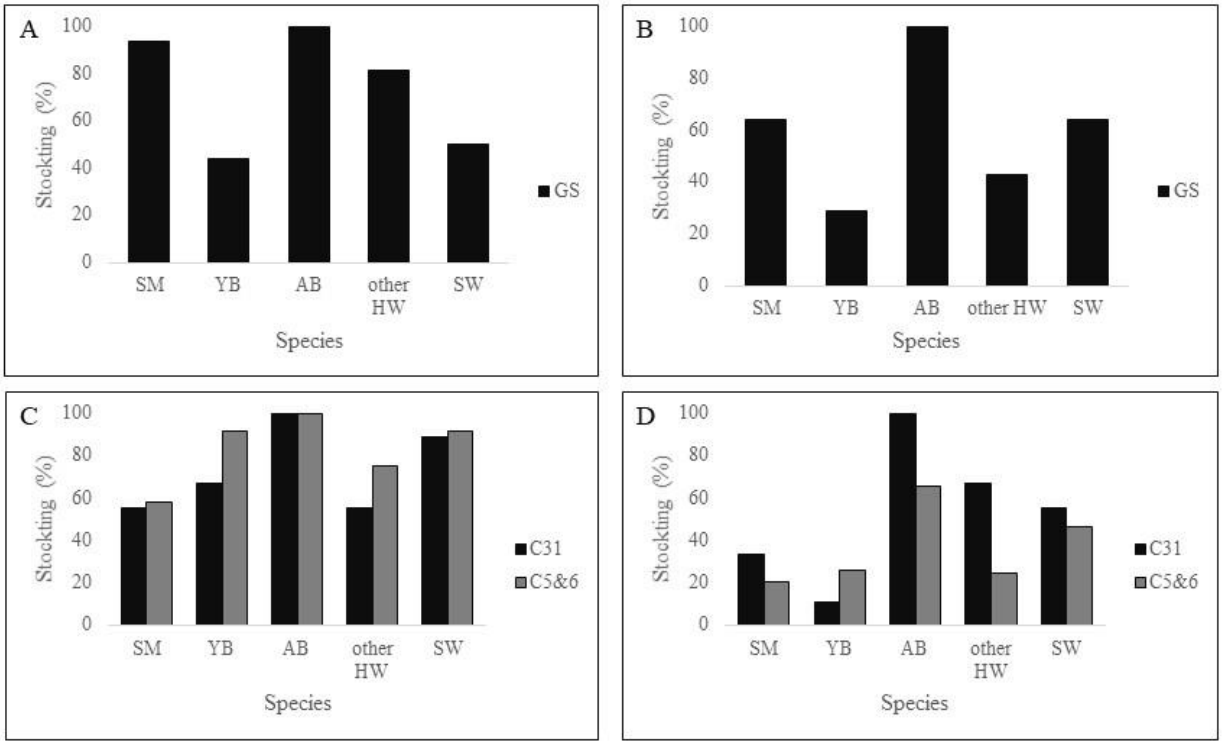

Figure 3-11. Regeneration stocking (%) for group selection treatments by forest for pre- and post-harvest inventories. Stocking presented by individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA, C and D: BEF.

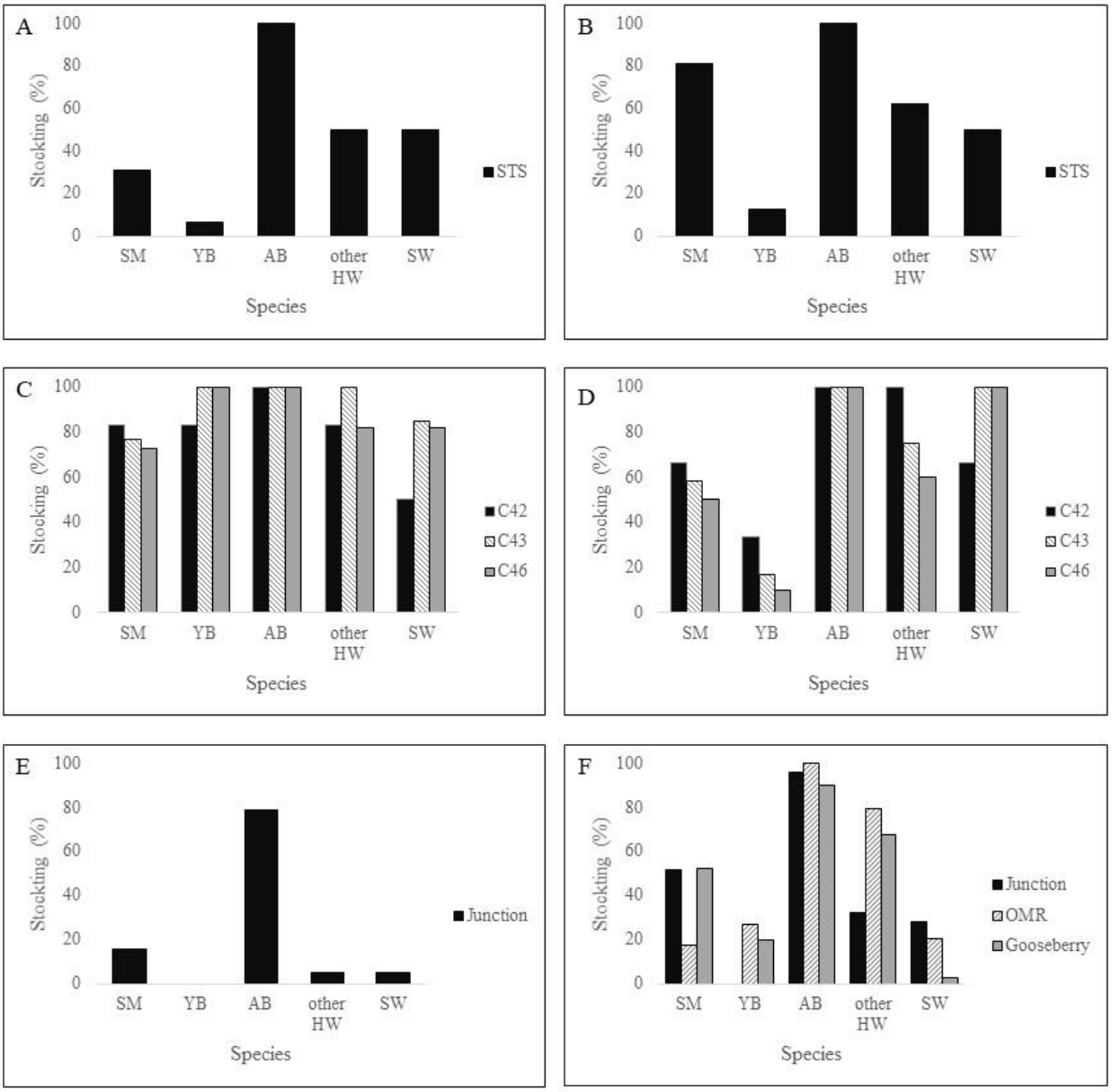

Figure 3-12. Regeneration stocking (%) for single-tree selection treatments by forest for pre- and post-harvest inventories. Stocking presented by individual species and species groups, SM (sugar maple), YB (yellow birch), AB (American beech), other HW (other hardwood species), and SW (softwood species). A and B: FERDA, C and D: BEF, E and F: HWF.

Tables

Table 3-1. Stand attributes by forest, stand, treatment and inventory

Treatment	Forest and Stand	Year	Inventory	Basal Area (m^2 ha^{-1})	Std. Error	Density (Trees ha^{-1})	Std. Error
Clearcut	FERDA: CC	1998	Pre	28.5	2.7	608.2	42.4
	FERDA: CC	2014	Post	1.9	0.3	194.5	31.2
Shelterwood	BEF: C35	1932	Pre	26.2	0.9	708.9	107.9
	BEF: C35	2002	Post	14.9	1.3	256.9	15.6
	FERDA: SW	1998	Pre	23.1	1.4	432.3	26.4
	FERDA: SW	2014	Post	7.6	1.2	126.6	22.1
	HWF: WL	2016	Post	21.6	0.8	713.5	40.6
Group Selection	BEF: C31	1932	Pre	24.6	1.4	566.5	46.9
	BEF: C31	2002	Post	22.4	3.6	466.6	77.4
	BEF: C5&6	1931	Pre	22.3	1.2	565.6	67.6
	BEF: C5&6	2017	Post	33.1	2.1	795.2	29.2
	FERDA: GS	1998	Pre	25.6	1.9	473.9	16.4
	FERDA: GS	2014	Post	20.7	2.1	413.7	33.3
Single-Tree Selection	BEF: C42	1932	Pre	24.7	1.5	698.2	17.4
	BEF: C42	2002	Post	29.3	2.4	505.5	62.7
	BEF: C43	1932	Pre	24.2	1.1	723.5	48.3
	BEF: C43	2002	Post	27.3	1.5	522.8	35.8
	BEF: C46	1932	Pre	24.8	1.2	698.8	53.7
	BEF: C46	2002	Post	25.1	2.4	573.0	107.6
	FERDA: STS	1998	Pre	33.0	2.7	552.7	30.0
	FERDA: STS	2014	Post	24.1	2.4	515.6	44.9
	HWF: JS	1988	Pre	34.3	2.6	1284.1	103.3
	HWF: JS	2016	Post	29.3	2.3	536.9	82.7
	HWF: OMR	2016	Post	20.8	0.8	425.4	39.8
	HWF: GM	2016	Post	21.6	0.9	541.1	47.0

Table 3-2. Species (HSpecies) and diameter (HDiam) diversity indices by forest, stand, treatment, and time.

Treatment	Forest and Stand	Year	Inventory	HDiam	HSpecies
Clearcut	FERDA: CC	1998	Pre	2.11	1.07
	FERDA: CC	2014	Post	0.48	0.85
Shelterwood	BEF: C35	1932	Pre	2.27	1.36
	BEF: C35	2002	Post	2.25	1.15
	FERDA: SW	1998	Pre	2.03	0.78
	FERDA: SW	2014	Post	1.02	0.62
	HWF: WL	2016	Post	1.56	0.97
Group Selection	BEF: C31	1932	Pre	2.37	1.13
	BEF: C31	2002	Post	2.29	0.94
	BEF: C5&6	1931	Pre	2.29	1.15
	BEF: C5&6	2017	Post	1.98	0.92
	FERDA: GS	1998	Pre	2.11	1.20
	FERDA: GS	2014	Post	1.90	1.06
Single-Tree Selection	BEF: C42	1932	Pre	2.24	1.10
	BEF: C42	2002	Post	2.49	1.07
	BEF: C43	1932	Pre	2.19	1.26
	BEF: C43	2002	Post	2.45	1.25
	BEF: C46	1932	Pre	2.24	1.25
	BEF: C46	2002	Post	2.26	1.06
	FERDA: STS	1998	Pre	2.25	0.98
	FERDA: STS	2014	Post	2.05	1.05
	HWF: JS	1988	Pre	1.57	1.07
	HWF: JS	2016	Post	1.66	0.93
	HWF: GM	2016	Post	1.46	0.74
	HWF: OMR	2016	Post	1.48	0.77

Table 3-3. Pre and post species composition of advance regeneration by forest, treatment, and stand. *Signals base condition.

Treatment	Forest	Inventory	Stand	SM	YB	AB	other HW	SW
Clearcut	FERDA	Pre	CC	19.6	1.2	57.6	20.1	1.5
	FERDA	Post	CC	4.0	27.5	20.3	46.3	1.9
Shelterwood	FERDA	Pre	SW	9.6	1.7	55.8	29.7	3.1
	FERDA	Post	SW	0.0	6.5	42.1	37.4	14.0
	BEF	Pre	C35	11.4	23.4	39.5	6.6	19.2
	BEF	Post	C35	8.9	8.9	28.6	8.9	44.6
	HWF	Pre	Junction*	20.4	0.0	64.0	14.0	1.6
	HWF	Post	Wolf Lake	39.6	8.3	45.4	6.3	0.4
Group Selection	FERDA	Pre	GS	15.0	3.6	44.8	31.5	5.1
	FERDA	Post	GS	7.2	2.1	72.3	7.7	10.8
	BEF	Pre	C31	2.0	3.2	63.3	2.8	28.7
	BEF	Post	C31	4.5	0.8	81.0	4.0	9.6
	BEF	Pre	C 5&6	5.2	12.7	45.4	7.6	29.1
	BEF	Post	C5&6	5.6	14.0	50.0	18.4	12.0
Single-Tree Selection	FERDA	Pre	STS	11.4	0.5	62.7	5.4	19.9
	FERDA	Post	STS	3.5	0.6	65.5	6.1	24.3
	BEF	Pre	C42	18.2	7.8	64.3	6.1	3.7
	BEF	Post	C42	1.5	1.8	66.0	16.6	14.1
	BEF	Pre	C43	12.4	20.4	34.4	14.9	17.9
	BEF	Post	C43	3.1	0.6	53.0	6.9	36.4
	BEF	Pre	C46	16.5	14.9	46.4	4.7	17.6
	BEF	Post	C46	2.2	0.2	54.4	3.6	39.7
	HWF	Pre	Junction*	20.4	0.0	64.0	14.0	1.6
	HWF	Post	Junction	22.8	0.0	61.9	7.4	7.9
	HWF	Post	OMR	2.6	2.3	70.4	21.7	3.1
	HWF	Post	OMR	2.6	2.3	70.4	21.7	3.1

Table 3-4. Classification of diameter distributions using the Janowiak et al. method (2008).

Forest and Stand	Treatment	Diameter Shape
BEF: 5&6	GS	Negative exponential
BEF: 31	GS	Variable
BEF: 42	STS	Negative exponential
BEF: 43	STS	Negative exponential
BEF: 46	STS	Rotated sigmoid
FERDA: GS	GS	Concave
FERDA: STS	STS	Concave
HWF: Junction	STS	Concave
HWF: GM	STS	Concave
HWF: OMR	STS	Rotated sigmoid

Table 3-5. Model outputs

Sugar Maple					
Random Effect					
Group	Variance	Std. Dev.			
Plot	0.20	0.45			
Stand	0.27	0.52			
Forest	2.02	1.42			
Fixed Effect					
	Estimate	Std. Error	Z-Value	P-Value	
Intercept	3.50	0.98	3.57		0.00
treatment: GS	-0.89	0.61	-1.47		0.14
treatment : STS	-1.41	0.57	-2.48		0.01
treatment: SW	-1.93	0.89	-2.17		0.03
Time	0.04	0.01	3.00		0.00

Yellow Birch				
Random Effect				
Group	Variance	Std. Dev.		
Plot	0.18	0.43		
Stand	2.11	1.45		
Forest	0.13	0.37		
Fixed Effect				
	Estimate	Std. Error	Z-Value	P-Value
Intercept	2.50	0.34	7.37	0.00
HDiam	-0.81	0.07	-11.16	< 2e-16
HSpecies	0.64	0.27	2.37	0.02
Time	0.04	0.02	2.21	0.03
Yellow Birch & Sugar Maple				
Random Effect				
Group	Variance	Std. Dev.		
Plot	0.11	0.33		
Stand	0.31	0.56		
Forest	1.26	1.12		
Fixed Effect				
	Estimate	Std. Error	Z-Value	P-Value
Intercept	4.20	0.85	4.92	0.00
HDiam	-0.54	0.16	-3.29	0.00
treatment: STS	-1.20	0.55	-2.19	0.03
treatment: SW	-1.55	0.67	-2.30	0.02
Time	0.04	0.01	3.02	0.00

Table 3-6. Model comparisons

Model	AIC	Correlation $(P : A)^2$
SM Full	2105	0.211
SM Reduced	2102	0.201
YB Full	NA	0.11
YB Reduced	NA	0.186
SM:YB Full	3456	0.109
SM:YB Reduced	3455	0.108

CHAPTER 4: LONG-TERM EVOLUTION OF COMPOSITION AND STRUCTURE AFTER REPEATED GROUP SELECTION OVER EIGHT DECADES

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4.1 Abstract

The selection system of silviculture has been used for centuries to maintain diverse stand structure and sustained yield over time. In northeastern North America, group selection is frequently used in northern hardwood forests to maintain uneven-age stand structure in conjunction with a range of shade tolerant and intolerant canopy tree species. For this study long-term results from the Bartlett Experimental Forest, New Hampshire, USA provided a unique opportunity to address cohort and stand level progression after repeated application of group selection over an 80-year period. Cohort-level structural and compositional development reflected successional and developmental dynamics associated with even-aged forest systems, whereas aggregate conditions at the stand-level were consistent with expectations for uneven-aged systems. As cohorts aged, diameter distributions progressed towards descending monotonic forms and species composition transitioned from higher importance of shade-intolerant species to tolerant species. Standing deadwood and downed woody material in cohorts also followed trajectories of aging even-age stands through time. Initial deadwood in younger cohorts was dominated by smaller stems of short-lived species while deadwood in older cohorts was comprised

of larger, more shade-tolerant species. Results also showed the development of regeneration through time. Increases in levels of non-beech regeneration were associated with declines in litter thickness and supported the hypothesis that leaf litter from American beech inhibits regeneration of more desirable species, specifically sugar maple and yellow birch. Although beech was a primary species across cohorts and at the stand level, stand level regeneration included a mixture of more commercially valuable species. Long-term results from this work offer new insight into the development of group selection treatments in northern hardwood stands. These insights fill a crucial knowledge gap needed for application of group selection to meet existing and evolving management objectives into the future.

4.2 Introduction

Uneven-aged silvicultural systems have been applied to a great range of forest types and ownerships throughout temperate regions of the globe. Use of these systems has fluctuated over time depending largely on public perceptions of more intensive even-age approaches (O'Hara, 2002; Pommerening and Murphy, 2004). The earliest forms of uneven-age management were developed in Europe during the1800s in response to rapidly diminishing wood supplies (Puettmann et al. 2009). These selection-based silvicultural systems promoted an all-aged stand structure in an attempt to achieve sustained yield over time (Baker 1934). A main assumption of these systems was that smaller, younger stems replaced mortality of older trees (Baker 1934). In addition to sustained yield, uneven-age systems also met secondary management objectives of protecting soil and water quality by maintaining continuous forest cover (Troup 1928, Guldin 1996, Miller and Kochenderfer 1998). Distinct age class characteristics of

uneven-age forests were established by single-tree or group removals guided by recommended residual diameter distributions. Structural guides associated with selection methods used in North America, including the BDq approach and Arbogast guide, pushed stands towards a reverse-J diameter distribution over time (Arbogast Jr, 1957; Guldin, 1991; O'Hara and Gersonde, 2004).

Today, selection-based silvicultural systems remain a dominant form of management in many regions (O'Hara 2002; Pommerening and Murphy 2004), due in large part to the consistency of these approaches with meeting policy mandates and contemporary objectives that favor the maintenance of mature forest habitat conditions (Fahey et al., 2018; Franklin, 1993; Franklin et al., 2002; LeDoux, 1999). Structural targets and sustained yield are still important management objectives, but in balance with aesthetic values, retention of coarse woody material and snags, species diversity, and resilience to changing conditions (D'Amato et al., 2011; Gamfeldt et al., 2013; Keeton, 2006; O'Hara, 1998). Despite the general notion that selection methods best satisfy more recent ecological objectives, long-term evaluations of these approaches suggest repeated application may lead to declines in important aspects of compositional and structural complexity, including loss of less tolerant canopy tree species and the abundance of coarse woody material (Kenefic and Nyland 2007, Webster and Jensen 2007, Gronewold et al. 2010, D'Amato et al. 2011). These unexpected dynamics underscore the importance of long-term evaluations for refining historical silvicultural approaches to satisfy contemporary and emerging objectives.

In northern hardwood forests in northeastern North America, selection methods have been widely applied to meet past and contemporary management objectives (Leak et

al., 2014, 1987; Nyland, 1998). These treatments largely mimic the frequent, partial canopy disturbances common in the region (Lorimer and White, 2003; Seymour et al., 2002) and have historically been successful in sustaining dominance of desired commercial species, namely sugar maple (*Acer saccharum).* In addition, the lower harvesting intensity of these methods relative to other silviculture systems is consistent with the objectives of the family forest owners who own much of the region's land base (Costello et al., 2000; Kelty et al., 2003).

Long-term studies in various regions within the range of northern hardwood forests have shown single-tree selection can successfully regenerate sugar maple (Bedard and Majcen, 2001; Crow et al., 2002; Eyre and Zillgitt, 1953; Gilbert and Jensen, 1958) and other species that rely on advance regeneration, particularly on more fertile soils (Bédard and Majcen, 2003; Neuendorff et al., 2007; Webster and Jensen, 2007). Nonetheless, long-term application has generally led to forest conditions dominated by shade-tolerant species in all canopy layers (Lamson and Smith 1991; Neise and Strong 1992). This transition is in stark contrast to the diversity of canopy species and tolerances characterizing natural, unmanaged examples of this forest type (Angers et al., 2005; Lorimer, 1977; Society, 2011; Woods, 2004). The decline in species diversity over time, including the loss of ecologically and commercially important mid-tolerants, such as yellow birch (*Betula allegehenesis*), has been a major critique of single-tree selection (Miller and Kochenderfer 1998; Webster and Jensen 2007). This issue has become increasingly problematic in stands with a heavy component of American beech (*Fagus grandifolia*) (Bohn and Nyland, 2003). Beech is a very shade-tolerant species and often becomes dominant with repeated single-tree selection cuttings (Canham, 2010; Jones et

al., 1989; Nyland et al., 2006). High populations of white-tailed deer (*Odocoileus virginianus)* can further exacerbate this problem, as sugar maple and yellow birch are preferred species for browse relative to beech (Godman et al. 1990).

The ecological and economic challenges associated with single-tree selection has increased attention to group selection methods as a potential strategy to balance operational efficiency and maintenance of species diversity (Leak 1996; Kellogg and Bettinger 1996; Kern et al. 2017). Given the larger gap sizes associated with this approach (0.04 ha to 0.8 ha), group selection often creates conditions more suitable for regeneration and establishment of mid-tolerant and intolerant species (Poulson and Platt, 1989; Poznanovic et al., 2013). In addition, the use of group removals may provide an advantage in accommodating the patchy (i.e., "irregular") structural and compositional conditions that have developed in these forests over time under prevailing natural disturbance regimes (Hanson and Lorimer, 2007), as well as following historical exploitive harvests (Kenefic and Nyland, 2006). Early research on northern hardwood silviculture acknowledged that maintaining yellow birch specifically would require integration of larger openings into forest stands (Eyre and Zillgitt, 1953; Gilbert and Jensen, 1958). The application of larger openings (> 0.04 ha) has proven critical for providing a competitive advantage for less-tolerant species over beech and sugar maple regeneration, especially if advance regeneration is removed and soils are scarified at the time of group removals (Leak et al., 2014; Shields et al., 2007).

Group selection may also offer productivity and operational benefits relative to single-tree section in terms of tree growth and marking efficiency. For example, work in northern hardwood systems in Wisconsin showed higher productivity in small group

openings up to a gap size of 100m^2 where productivity reached an asymptote (Webster and Lorimer, 2005). In addition, implementing single-tree selection is often viewed as less efficient than group selection, as marking decisions for group selection are often driven by presence of desirable advance regeneration and/or groups of economically mature trees (Leak and Gottsacker, 1985), whereas single-tree marking focuses more on individual tree assessments of quality, risk, and financial or biological maturity (Havreljuk et al., 2014). This flexibility in application, combined with higher potential for species diversity, has made group selection a valuable tool for meeting increasingly diverse management objectives, including adapting to changing forest health and social conditions (Battles et al., 2001; Mutch et al., 1993; Reuling et al., 2019).

One of the longest continuously maintained studies of group selection in the USA is at the Bartlett Experimental Forest in Bartlett, New Hampshire where group selection has been repeatedly applied to a 46-ha northern hardwood stand since the late 1930s (Leak and Filip, 1977). Results from the first 61 years of the study showed an increased component of mid and intolerant species, yellow birch, paper birch (*Betula papyrifera*), and white ash (*Fraxinus americana*), in the sapling and small pole size classes (Leak, 1999), despite strong beech dominance in the pre-treatment stand. These results have led to an increased reliance on group selection harvests across northeastern North America to serve as a technique to transition even-aged forests to uneven-aged conditions (Kelty et al. 2003) and to maintain compositional diversity in uneven-aged forests dominated primarily by shade-tolerant species like beech and sugar maple (Falk et al., 2010; Kern et al., 2017)

Despite the broad application of group selection, key knowledge gaps remain regarding the long-term outcomes of this approach on stand-level structure and composition. This study takes advantage of the unique abovementioned long-term study at the Bartlett Experimental Forest to examine the outcomes of eight decades of group selection harvests on stand evolution and individual cohort development. Much of our knowledge regarding the outcomes of repeated group selection emphasizes stand-level changes, leaving a limited understanding of within-stand variability, particularly structural and compositional conditions. Given group selection is often applied by extending even-aged concepts of area regulation to allocating and tracking within-stand cohort area and distribution, there is value in understanding the influence of cohort-level development on overall stand conditions. With this work we undertook a detailed analysis of gap cohort development over time relative to the surrounding matrix and broader stand. Specifically, we classify changes in compositional and structural attributes, regeneration, mortality, and growth of cohorts created by group selection over time. This work will address five hypotheses regarding emergent stand and cohort properties: 1) Emergent stand properties as they relate to structure, composition, regeneration, and sustained yield meet the objectives of group selection (reverse-J diameter distribution, representation of less tolerant species in the overstory, desired species of advance regeneration, and consistent yield), 2) Species richness decreases as cohorts age, primarily due to loss of intolerant and mid-tolerant species over time, 3) Structural diversity in terms of live tree size distributions and the abundance of coarse woody material increases as cohorts age, 4) Cohort development in uneven-age stands managed with group selection reflects the cumulative effect of even-age cohorts, 5)

Long-term regeneration dynamics of desired species, namely sugar maple, are associated with changes in leaf litter depth due to shifts in overstory composition and prevailing litter type.

4.3 Materials and Methods

4.3.1 Study Site

This research was conducted on a tract of uneven-aged northern hardwood forest at the Bartlett Experimental Forest in Bartlett, New Hampshire (44°17′N, 71°3′W). Group selection has been repeatedly applied to this stand, known as Compartments 5 and 6, since 1937. The initial harvest occurred from 1937 to 1940 with subsequent entries in 1951, 1960, and between 1992 and 1994. Group openings from these harvests ranged from 0.04 ha to 0.8 ha, with the average opening 0.2 ha in size (Figure 4-1). Following the harvest in the early 1990s, 46% of the stand had been treated with group selection (Table 4-1).

The areas examined are at approximately 427 m in elevation and soils are primarily sandy loam podzols derived from glacial drift (McClure 1990; Leak 1999). Climate is categorized by moderate summers and cold winters with snow coverage from December through mid-April (McClure 1990). The initial composition was approximately 70% shade-tolerant species (beech, sugar maple, eastern hemlock [*Tsuga canadensis*], and red spruce *[Picea rubens*]), 25% mid-tolerant species (yellow birch, red maple [*Acer rubrum*], white ash), and 5% intolerant species (primarily paper birch). Harvesting in the stand prior to the establishment of this experiment in the late 1930s was

limited to light high-grading for softwood species, namely red spruce, at the turn of the century (Leak and Filip, 1977).

During the first entry, groups were clustered in areas containing mature trees with softwood advance regeneration and saplings up to 15.2 cm diameter at breast height (dbh) retained where present (Leak and Filip, 1977). Later entries were treated as small clearcuts (Gilbert and Jensen, 1958), removing nearly all existing woody vegetation within the group, including advance regeneration of beech, with group establishment focused in areas containing mature or over mature trees (Leak, 1999).

4.3.2 Plot Selection

In 2017, 81 sample plots were established across the stand using a stratified sample design proportional to area of each cohort. Plot count per cohort was proportional to area, in hectares, based on the following guidelines, 10% sample from each cohort created through harvesting (four in total) and a 5% sample from the matrix (i.e., unmanaged) cohort. Plots were 0.04 ha circular, fixed area plots (Appendix). Area of the managed cohorts was calculated in ArcGIS (https://www.arcgis.com) using digitized maps of group openings. Area of the matrix cohort was the difference between the total stand area and area in groups. For each managed cohort, all groups were binned into 0.04 ha area classes. One group from each area class was randomly selected for sampling using the random point function in ArcGIS. One plot was placed in the middle of each selected group; two plots with centers 75 m apart were established in groups larger than 0.4 ha in size. After groups were selected from each area class, plots were located in randomly selected groups across all area classes until the 10% sample was complete. For

the matrix cohort, plots were established using a 40.2 m by 40.2 m grid with a random start. Plots were not included in the final sample if they fell within 20.1 m of a group or the stand edge.

Groups included in the final sample were located in the field using a handheld GPS. Fixed-area plots were established at the group center using ArcGIS with locations visually confirmed in the field by walking the group perimeter.

4.3.3 Plot Measurements

Overstory trees ($\geq$ 10.2 cm dbh) were measured on the 0.04 ha plots, saplings ($\geq$ 2.5 cm <10.2 cm dbh) were measured on 0.02 ha nested circular plot, and seedlings were measured in four 0.0004 ha plots. Diameter and species were recorded for all live and dead overstory trees. For saplings, dbh and species were recorded.

Seedling plots were located 5 m out from plot center at azimuths of 0, 90, 180, and 270°. Seedlings were tallied by species and size class from 0.3 m in height to 2.54 cm dbh. Size classes were grouped as follows; 0.3 m to 0.9 m, 0.9 m to 1.8 m, 1.8 m to 2.54 cm dbh. In addition to seedling measurements, litter depth and percent cover of understory vegetation was recorded in each nested seedling plot.

Downed woody material was measured for wood pieces $\geq$ 10 cm in diameter and > 1 m in length following the line intercept method (Harmon and Sexton, 1996). Diameter at intercept, species, where possible, and decay class based on Sollins (1982) were recorded for coarse wood pieces intersected.

4.3.4 Statistical Analysis

Analysis for this work was conducted at the cohort and stand scale. Cohorts were summarized as follows, the 1990s cohort are the group selection harvests created between 1992 – 1994, 1960s cohort corresponds to the groups created in 1960, 1950s cohort are the groups established in 1951, the 1930s cohort are the original groups, corresponding to the entry between 1937 – 1940, and the matrix cohort is the surrounding portion of the stand not cut with group selection. This cohort level grouping was used for a chronosequence analysis where age increases from youngest cohort (1990s cohort) to oldest managed cohort (1930s cohort), and with the matrix cohort representing the oldest, unmanaged stand condition.

For each cohort, overstory characteristics related to structure, composition, and development were calculated. Overstory trees were classified as those ≥ 10.2 cm at breast height. Overstory structure was assessed using density, basal area, stand density index, Shannon's diversity index for size classes, and standing dead and downed woody material. Density was calculated as the number of trees per hectare in each 5-cm size class by species group (beech, sugar maple, yellow birch, eastern hemlock, and other species) and total. Shape of the total diameter distribution was classified following the approach developed by Janowiak et al. (2008).

Stand density index (SDI) for each cohort was determined using the additive method by species group:

$$SDI = \sum \left(\frac{Di}{10}\right)^{1.6}$$

Where *Di* is the quadratic mean diameter for each cohort and species group (Shaw 2000). The 99th percentile maximum SDI, SDI_{99}, was determined based on Woodall et al. (2005) using specific gravity of each species :

$$E(SDI_{99}) = b_0 + b_1(SG_m) + e$$

Where $E(.)$ is the statistical expectation, b_0 and b_1 are the estimated parameters, SG_m is the mean specific gravity based on values from Ducey and Knapp (2010), and e is the random error term. Relative density was calculated from Woodall et al.(2006) to compare the relationship between SDI and SDI_{99} for each cohort. Shannon's diversity index was determined for density by diameter class of each cohort using the diversity function in the vegan package of R (https://www.r-project.org/). Greater values of Shannon's diversity index (HDiam) correspond to greater diversity in size classes.

Standing dead trees per product class were calculated by basal area as well as volume of downed woody material. Product classes were divided into three groups, saplings (2.5 to 10.1 cm), poletimber (10.2 to 21.3 cm), and sawtimber (≥ 21.4 cm). Woody material volume was computed using the following formula:

$$V = (\frac{\pi^2 \Sigma d^2}{8L})*10000$$

Where V is the volume of coarse woody material ($m^3\ ha^{-1}$), d is the diameter of the woody material (m), and L is the transect length (m) (van Wagner 1968).
To track compositional change over time species importance values were calculated for the same species groups listed above using the following formula:

$$IV = (RDen + RDom)/2$$

Where RDen is the relative density of a single species measured in trees per hectare and RDom is the relative dominance of a species measured by basal area in m^2 ha^{-1}.

Development of cohorts was evaluated using periodic annual increment (PAI) of live trees and mortality rates. As we did not have repeated measurements of individual cohorts, cohort groupings were instead used to characterize cohort-level PAI and mortality using the following approaches PAI was calculated for live overstory trees as:

$$PAI = {BA_{t0} - BA_{t-1}}/{t_0 - t_1}$$

Where BA_{t-1} is basal area (m^2ha^{-1}) for the cohort year of interest and BA_{t0} is basal area for the previous measurement period (i.e., cohort).

Mortality rates were determined from the method developed by Sheil and May (1996):

$$1 - \left[1 - \left(\frac{M_1}{N_0}\right)\right]^{1/t}$$

Where M_1 is the total mortality using density (stems ha^{-1}), of a given cohort period, and N_0 is the total live density in the next oldest cohort period. t is the number of years between cohort periods.

Density and stocking of advance regeneration of American beech, sugar maple, yellow birch, and all other species was determined for each cohort. Advance regeneration was classified as seedlings and saplings ≥ 30.5 cm in height and up to 10.1 cm dbh. Density of seedlings for the same species groups were calculated for trees < 30.5 cm in height.

To compare stand to cohort evolution, stand-level basal area, density, mortality, and standing and downed woody material were also calculated following the methods outlined above.

Finally, the relationship between seedlings and beech leaf litter was explored using graphical analysis. At the plot level, seedling density of desired commercial species (sugar maple and yellow birch) was plotted against litter depth (cm) and litter depth was plotted as function of beech basal area. Simple linear regression lines were plotted on the data to show trends and 95% confidence intervals. Average cohort litter depth was also computed. Exploration of these relationships was based on previous hypotheses that sugar maple and yellow birch regeneration success improves in the absence of dense beech leaf litter (Hane et al., 2003; Leak, 2005).

A complete list of cohort and stand level variables calculated for this analysis is listed in the Appendix.

4.4 Results

4.4.1 Stand Scale

Total stand basal area was 33.1 ± 18.8 $m^2 ha^{-1}$ and live-tree size distribution followed a rotated sigmoid distribution after 80 years of group selection harvest (Appendix) with overstory trees ranging from 10 to 90 cm in size (Figure 4-2). Eastern hemlock was the most abundant species across size classes followed by American beech. Eastern hemlock also had the highest importance values and pin cherry the lowest (Table 4-2). Advance regeneration of beech was found on nearly all plots sampled while stocking of sugar maple and yellow birch was 51.0% and 36.2%, respectively (Table 4-

3). Density of advance regeneration and seedlings also varied by species, but American beech was the most abundant (Table 4-3).

Stand-level growth was positive across managed cohorts with an average growth rate of 0.52 $m^2ha^{-1}year^{-1}$ over the 80-year period examined. The average mortality rate at the stand scale over this period was 0.008 stems $ha^{-1}year^{-1}$.

4.4.2 Cohort Scale

At the individual cohort level, overstory basal area ranged from 10 $m^2\,ha^{-1}$ in the 1990s cohort to 50 $m^2\,ha^{-1}$ in the matrix cohort (Figure 4-3). Diameter distributions were truncated in the 1990s and 1960s cohort but moved towards a reverse-J shape as the cohorts aged (Figure 4-4). The weighted average stand structure showed the 1990s cohort largely contributing to the smaller size classes, whereas larger size classes were primarily composed of trees from the matrix cohort (Figure 4-5). The diversity in stand structure, as measured by Shannon's diversity index, also increased as cohorts aged (Table 4-4). American beech was a dominant species across cohorts, whereas eastern hemlock increased in species importance as cohorts aged (Figure 4-6). Sugar maple was only marginally important in the 1990s cohort but increased in dominance between the 1960s and 1930s cohorts. Yellow birch was also an important species between the 1990s and 1930s cohort and was less abundant in the matrix cohort. Paper birch was most important in the 1960s cohort but decreased by the 1950s cohort.

Average SDI was similar between cohorts, ranging from 451.1 to 719.4, except for the 1990s cohort where average SDI was substantially lower (Figure 4-7A). SDI_{99} ranged from 1218.2 to 1283.4 for the 1990s to 1930s, respectively (Figure 4-7B). SDI_{99}

in the matrix cohort was significantly higher, with an average of 1732.7. Average relative density was lower in the 1990s cohort, at 0.16, than older cohorts where average RD was between 0.37 and 0.44 (Figure 4-7C).

Basal area of standing dead trees increased as cohorts aged, as did proportion of standing dead trees in the sawtimber product class (Figure 4-8). In the 1990s cohort, the majority of standing dead trees were in the sapling size class with a small portion in poletimber. Downed woody material volume was also lowest in the 1990s cohort. As cohorts aged the amount of beech DWM increased (Figure 4-9). Paper birch and pin cherry DWM was highest in the 1960s cohort (Figure 4-9).

Density of advance regeneration averaged 8,855 trees per hectare for all cohorts except the matrix where abundance of regeneration was below 1,800 trees per hectare (Figure 4-10). American beech was the most prolific species regenerating, although sugar maple and yellow birch advance regeneration was found in all cohorts except the matrix. Litter depth varied by cohort, ranging from 1.76 cm to 2.86 cm across cohorts, litter depth increased with increasing basal area of beech (Figure 4-11). Seedling density of sugar maple and yellow birch stems showed a slightly decreasing trend as leaf litter depth increased (Figure 4-12).

4.5 Discussion

Uneven-age management, specifically group selection, is a widely applied silvicultural approach to maintain diverse species and structural attributes in northern hardwoods (He et al. 2000) and other forests around the globe (Madsen and Hahn 2008). As management objectives broaden to included greater ecological and societal outputs, group selection is increasingly regarded as a silvicultural system with the necessary

flexibility to meet these contemporary goals (Lahde et al. 1999). Several long-term studies on group selection exist (e.g., Campbell et al. 2007, Homyackand Haas 2009); however, few cover the same duration of consistent treatment as this work or have explored the evolution of stands and individual cohorts over time. This study evaluates 80 years of management, providing an invaluable look at the long-term sustainability of group selection for meeting historical and current objectives, particularly in forests containing a recalcitrant beech understory.

4.5.1 Emergent stand properties

Management of forests under group selection revolves around assumptions of sustained yield, retention of desired species, and ample regeneration for future cohorts (Minckler 1972, Leak and Gottsacker 1985). Findings from this work support our hypotheses that these assumptions can be met with repeated application of group selection cuttings over time. Following 80 years of management, emergent stand structure was classified by a rotated sigmoid diameter distribution (Appendix). Previous findings from this study reported a reverse-J diameter distribution, although this shape was not confirmed statistically (Leak and Filip 1977; Leak 1999). The reverse-J distribution has long been the benchmark for uneven-age silviculture (Guldin 1991) as it was theorized to represent a balanced stand condition where growth matches yield on a constant interval (Meyer 1952). However, the balanced stand condition was originally intended as a landscape scale metric rather than a guide for every stand (Meyer 1952). Other diameter distributions, including the rotated-sigmoid and increasing-*q*, have been observed in old growth and managed uneven-aged northern hardwoods (Goff and West

1975; Leak 1996; Neuendorff et al. 2007, Gove et al. 2013). The variable shape of these distributions more likely mimics natural development of forests and an associated u-shaped trend in mortality rates (Lorimer et al. 2001) relative to the balanced reverse-J distribution (Goff and West 1975, Lorimer and Frelich 1984, Goodburn and Lorimer 1999).

An underlying assumption of the reverse-J distribution is the equal allocation of growing space to each cohort in a stand (Smith et al. 1997). Application of group selection in the areas examined at the BEF was consistent with this assumption and intentionally allocated growing space to each cohort; the negative exponential distribution previously observed likely reflected this (Leak 1999). Deviation from this form in our current assessment may be due to the long time period (25 years) since the last harvest entry, which allowed for increased development and stocking of the small to medium sawtimber size classes. Detection of a reverse-J shaped distribution is also sample-size dependent with previous work from northern hardwoods in the Lake States region demonstrating a sample area of at least 13% of the stand was needed to detect the true underlying diameter distribution (Janowiak et al., 2008). For our analysis, we sampled 15% of the compartment area suggesting sampling was adequate for detection of the true curve form. Although this form does not conform to theoretical distributions historically suggested for uneven-aged management, there are ecological and economic advantages of rotated sigmoid structures given the higher stocking of larger diameter trees with this form (Keeton 2006), including small sawtimber size classes, which have the greatest potential for increase in tree grade over each cutting cycle (Mendel et al., 1973).

As with structural diversity and sustained yield, our findings support the hypothesis that group selection can maintain species diversity over time. At the stand scale, the species with the highest importance values are also the most shade tolerant (Table 4-2), although shade-intolerant species including paper birch and pin cherry are still present throughout the stand. The high importance of eastern hemlock is due to the large portion of the stand in the matrix cohort and the initial practice of retaining advance softwood regeneration in groups. The importance of beech relative to more desirable and less shade-tolerant species like sugar maple and yellow birch may also be a relic of past management. In earlier cohorts, group openings were smaller on average than openings in younger cohorts (Table 4-1). For more shade-intolerant species, regeneration failure is likely unless gaps are large (Malcolm et al. 2001), as smaller openings may not provide the gradient of resource availability, primarily light and moisture, from gap center to edge required to recruit a range of tolerances (York et al. 2002). Given average gap size has increased over the duration of the study, species importance values may shift as younger cohorts transition from sapling to overstory size classes.

At the stand scale we also observed ample stocking and density of desired species, including less shade-tolerant species, such as yellow birch (Table 4-4). Although beech stocking is nearly 100%, sugar maple and yellow birch regeneration were still present as seedlings and as advance regeneration (Table 4-4). Retention of these species, especially as advance regeneration, is essential for future management and a key assumption in the application of group selection in northern hardwoods (Leak 1999; Leak et al. 2014). The balance of regeneration from a range of species shade tolerances also more closely mimics the natural dynamics of these forests, which are characterized by a

mix of frequent gap scale and less frequent mesoscale disturbances, such as wind storms that generate a range of light and microsite conditions (Hanson and Lorimer, 2007). The variability in harvest opening size associated with group selection relative to single-tree selection is expected to provide conditions that overlap with more species niches (Grubber 1977; Perala and Alm 1990, Shields et al. 2007). For this work we did not compare regeneration response with gap size directly, although that relationship has been discussed in other studies of group selection (McDonald and Abbott 1994; Weigel and Parker 1997) and may be more accurately addressed in our cohort analysis.

4.5.2 Cohort Properties

Species diversity at the stand scale after repeated group selection was the cumulative effect of distinct species composition within cohorts with cohort-scale composition changing with time since harvest (Figure 4-6). In the youngest cohort (the 1990s), species importance values reflected early successional characteristics with greater abundance of shade-intolerant and mid tolerant species (pin cherry, paper birch, and yellow birch). As cohorts aged, the importance of shade tolerant species increased (American beech, eastern hemlock, and sugar maple). These shifting compositional dynamics highlight the longevity and growth strategies of individual species. For example, the changing importance of paper birch over time represents a clear example of cohorts capturing unique aspects of a given species development. There is a marked drop in the importance of paper birch and a corresponding increase in the volume of paper birch DWM between the 1960s and 1950s cohorts (Figure 4-6, Figure 4-9). These results likely reflect the short-lived, early successional nature of paper birch and denote when

intermediate and long-lived species become more dominant in the stand (Safford et al. 1990). The developmental strategy of sugar maple is also evident from changing importance values between cohorts. Sugar maple is nearly non-existent in the 1990s cohort but is a major component of the overstory by the 1950s cohort. This emergence of sugar maple in the stand several decades after harvesting has previously been observed at the BEF (Leak 2005) and is likely due to an increase in favorable sugar maple seedbed conditions as cohorts age (see *Regeneration* section below). The shift in dominance towards shade-tolerant species in older cohorts supports our hypothesis that species richness decreases over time due to loss of less tolerant species.

As with species composition and diversity, stand structure reflected the combined effect of different structural conditions within individual cohorts (Figure 4-4, Figure 4-5). The steep initial shape of the overall stand curve is driven by the high density of small stems in the youngest, 1990s, cohort (Figure 4-4 A-E, Figure 4-5). Similarly, the long tail of the diameter distribution is pulled by the oldest cohort: the matrix and 1930s. McGee et al. (1999) found similar evolution of overstory structure looking at the changes in diameter distributions between maturing, partially cut, and old-growth northern hardwoods stands in the Adirondack region of New York (1999). The increasing value of H_{Diam} as cohorts age also demonstrates greater structural diversity with time as was expected (Table 3).

4.5.3 Successional and Structural Evolution Over Time

In the context of stand dynamics, uneven-age management is associated with later stages of stand development, including understory reiniation and old growth (Guldin

1996, Oliver and Larson). However, the distinct structural and compositional conditions of each cohort suggest earlier developmental stages are also represented throughout the stand. Stem exclusion or the aggradation phase, for example, are more commonly associated with repopulation following stand replacing disturbances or even-age regeneration methods (Borman and Likens 1979, Oliver 1981, Oliver and Larson). However, the high density of small stems and sapling mortality in the 1990s cohort are in line with characteristics of these earlier successional stages (Figure 4-4, Figure 4-6). We tried to quantify differences in development between cohorts further using stocking metrics more commonly applied to even-aged stands, SDI and RD (Figure 4-7). Average SDI and RD were similar between all cohorts, except for the 1990s cohort which had significantly lower values. Based on RD, the 1990s cohort is beginning the onset of competition and other cohorts are between the lower limits of site occupancy and self-thinning (Long and Daniel 1990), suggesting the 1990s cohort is in stand initiation and other cohorts are in stem exclusion (Oliver and Larson 1996). Yet, when these classifications are considered alongside other metrics, including stand density, change in species composition, overstory mortality, and regeneration (Figure 4- 4, Figure 4-6, Figure 4-7, Figure 4-10), they are better classified as later developmental stages. For example, the presence of established regeneration, increasing dominance of more shade-tolerant species, and range of overstory diameters suggest the 1960s to 1930s cohorts are in the transitional phase before old growth (Borman and Likens 1979, Oliver and Larson 1990). Likely, the lower values of RD reflect the elevated values for SDI_{99} and the difficulty in accurately capturing maximum density in mixed species, mixed-age stands (Shaw n.d.; Woodall et al. 2003, 2005). As such, the SDI and RD values are most useful

for relative comparisons between cohorts. These findings demonstrate that gap-dynamics can mimic successional development generally attributed to even-age conditions and ultimately support our hypothesis that the uneven-age stand maintained by group selection is the cumulative effect of many smaller even-aged “stands”.

4.5.4 Regeneration

Differences between cohorts extend to the regeneration layer, although natural regeneration was abundant across all managed cohorts and exceeded 6000 stems ha^{-1} (Figure 4-10). Density of advance regeneration was substantially lower in the matrix cohort and comprised primarily of eastern hemlock and beech, two extremely shade tolerant species which can persist in the understory for long periods of time. Under group selection, it is assumed a new cohort of desired species will establish at each entry. Overstory species importance values, primarily the presence of sugar maple and yellow birch decades after harvest, support this assumption (Figure 4-5). The relationships between litter depth and regeneration of these species lends further support to the importance of changes in litter quality in affecting regeneration dynamics of sugar maple and yellow birch. For yellow birch, access to mineral soil is important for regeneration survival (Godman and Krefting 1960) and these conditions were created by harvesting equipment at the time of group creation. For sugar maple, regeneration occurs on leaf litter, although the seedling radical must be able to reach mineral soil during the moist period of the growing season (Godman et al. 1990). In stands with high populations of beech, litter depths often increase due to the elevated lignin content in leaves relative to other hardwood species (Melillo et al. 1982) leading to the inhibition of regeneration for

other species (Molofsky and Augspruger 1992; Dalling and Hubbell 2002). In addition, beech litter has been observed to chemically inhibit regeneration of other species (Hane et al., 2003; Leak, 2005). The increase in sugar maple dominance we observed in older cohorts may reflect change in litter quality over time in groups dominated by species with nutrient rich foliage, such as pin cherry, white ash, and yellow birch (Leak 2005). Although we did not classify litter composition in the field, the increase in litter depth with increasing beech basal area and the subsequent reduction of desired regeneration underscores an important dynamic that should be considered if goals include establishment and maintenance of sugar maple and yellow birch in these systems. Early cohort dominance by pin cherry, birch, ash and other species with higher litter quality ultimately result in reduced litter depths relative to sites dominated by beech and provide an important pathway for reestablishment of sugar maple in these areas over time.

4.5.5 Contemporary Objectives and Future Challenges

At the time of this study's establishment, goals were to maintain a mixture of species and range of size classes, from regeneration to mature overstory trees (BEF study plan). It is important to consider these goals and the current state of the stand in the context of regional conditions and additional management activity. The study area is in a region where white-tailed deer populations are comparatively lower than other parts of northeastern North American and, as such, precautions were not taken to prevent browsing. In regions with elevated deer populations some direct benefits from gap creation, including increased light availability, may be mitigated (Gasser et al., 2010; Kern et al., 2012). Additionally, all beech was felled during later harvests at the BEF,

which served to reduce beech composition relative to other studies where beech was not explicitly removed (Leak 1996). Group selection remains a viable option to meet many contemporary management objectives; however, modifications that better integrate structural legacies historically associated with gap disturbances in these systems may be necessary to achieve some ecological objectives. This includes retention of DWM and legacy trees within groups to maintain and increase structural diversity (Bolton and D'Amato 2011; Hanson et al. 2012; Klingsporn et al. 2012) however, within-group retention of living trees may need to be coupled with larger group openings to ensure suitable light conditions are still created for less tolerant species (D'Amato et al., 2015). Increasing structural, compositional, and functional diversity represents a strategy to better meet multiple objectives, including those for wildlife habitat and carbon storage (Gamfeldt et al., 2013). Such conditions are also regarded as an approach to address future uncertainty in environmental and forest health conditions (D'Amato et al., 2011) and satisfy policy guidelines for ecological and diversity oriented silviculture (Lahde et al. 1999, Harvey et al. 2002). Group selection, as practiced over the past eight decades at the BEF, has demonstrated the potential for this approach to sustain these desirable attributes relative to single-tree selection and some even-age methods in northern hardwood forests.

4.6 Conclusions

This study provides a unique evaluation of stand and cohort level dynamics after repeated group selection. Findings support past conclusions that group selection cuttings maintains an uneven-age condition while retaining species diversity across size classes. This work also highlights that the uneven-age status of the stand is the cumulative effect

of many small even-age “stands” created during each harvest. These findings underscore the ability of group selection to meet traditional management goals, such as sustained yield of quality species over time, but also emphasize the flexibility of this silvicultural system to address the increasingly diverse demands placed on forests. Ultimately, these findings capture changing dynamics important for management of northern hardwood forests, such as shifts in species composition, dominance by American beech, litter input, and structural evolution, not evident in the short-term. The long-term nature of this study provides a unique predictive framework for anticipating stand level conditions into the future with repeated group selection.

4.7 Works Cited

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Figures

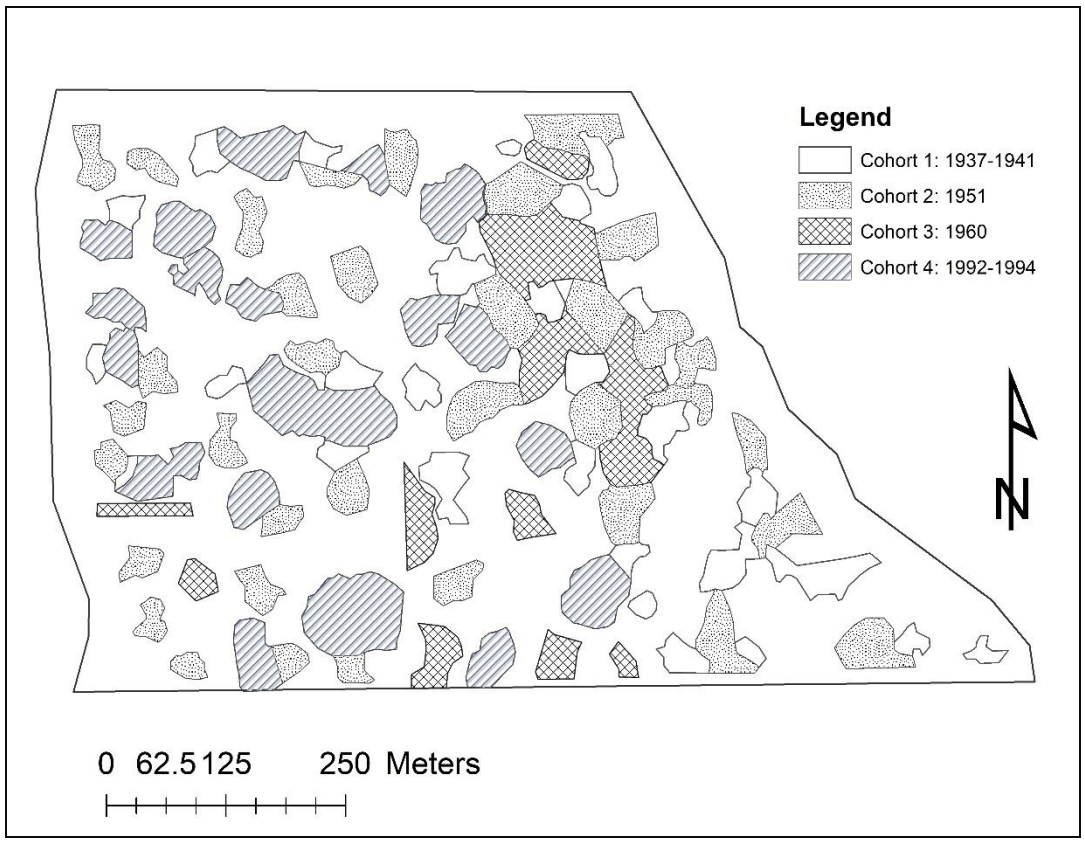

Figure 4-1. Group openings in the in Compartments 5 & 6 at the Bartlett Experimental Forest, New Hampshire, USA. Different patterns represent different cohorts created by application of group selection from 1937-1994. The matrix cohort is all area outside of groups.

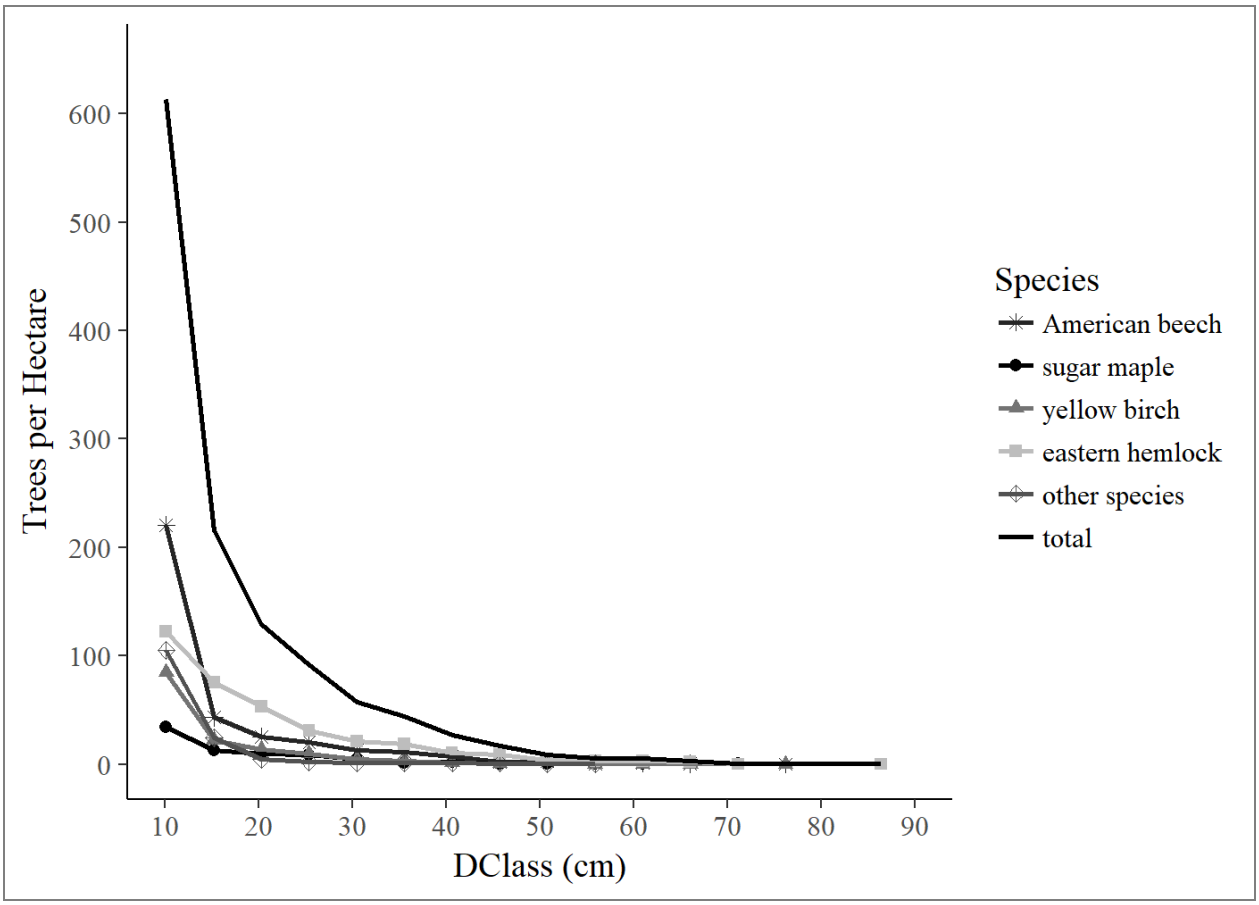

Figure 4-2. Stand-level, live-tree size distribution across species.

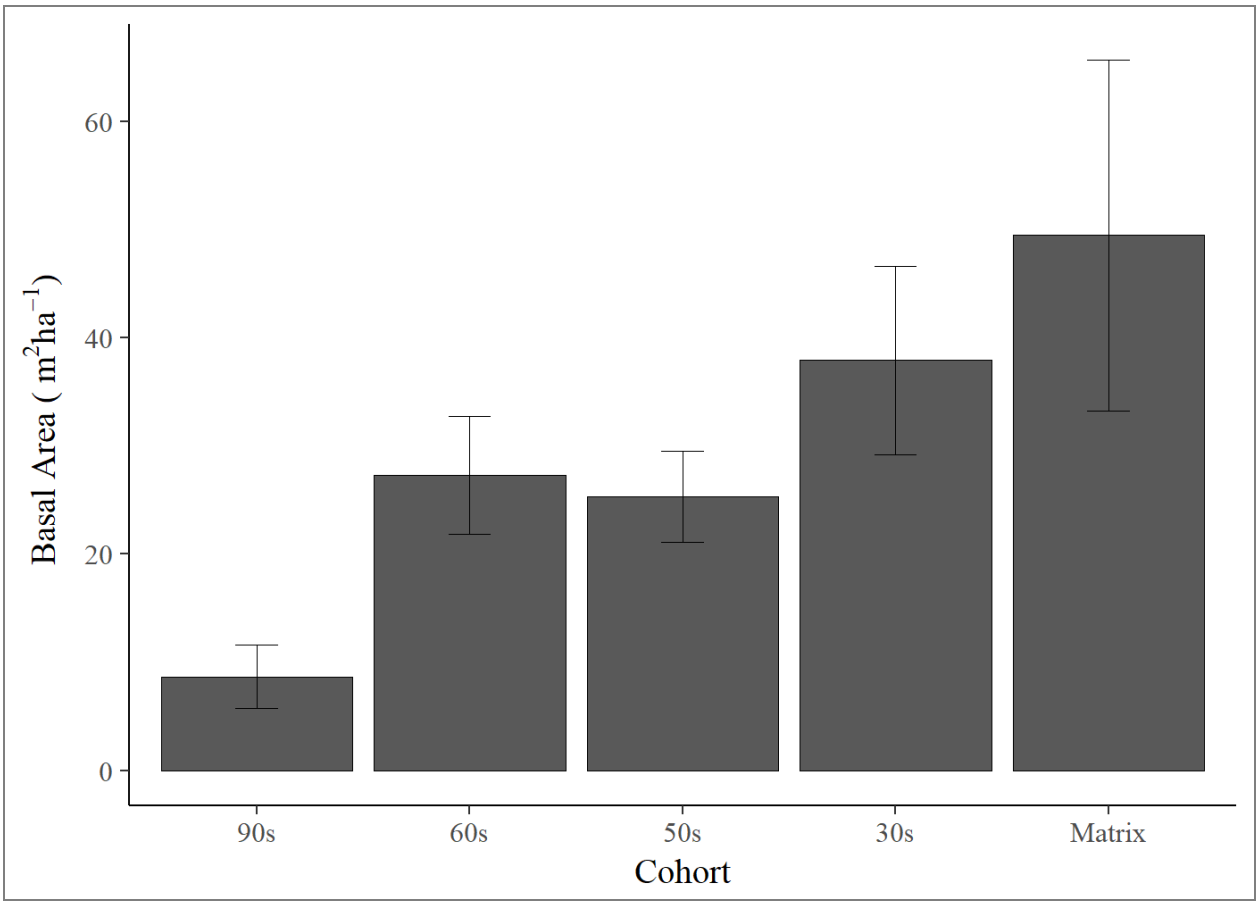

Figure 4-3. Overstory basal area m2 ha-1 by cohort. Cohort age increases from left to right. Stand wide basal area was 33.1 ±18.8 m2ha-1.

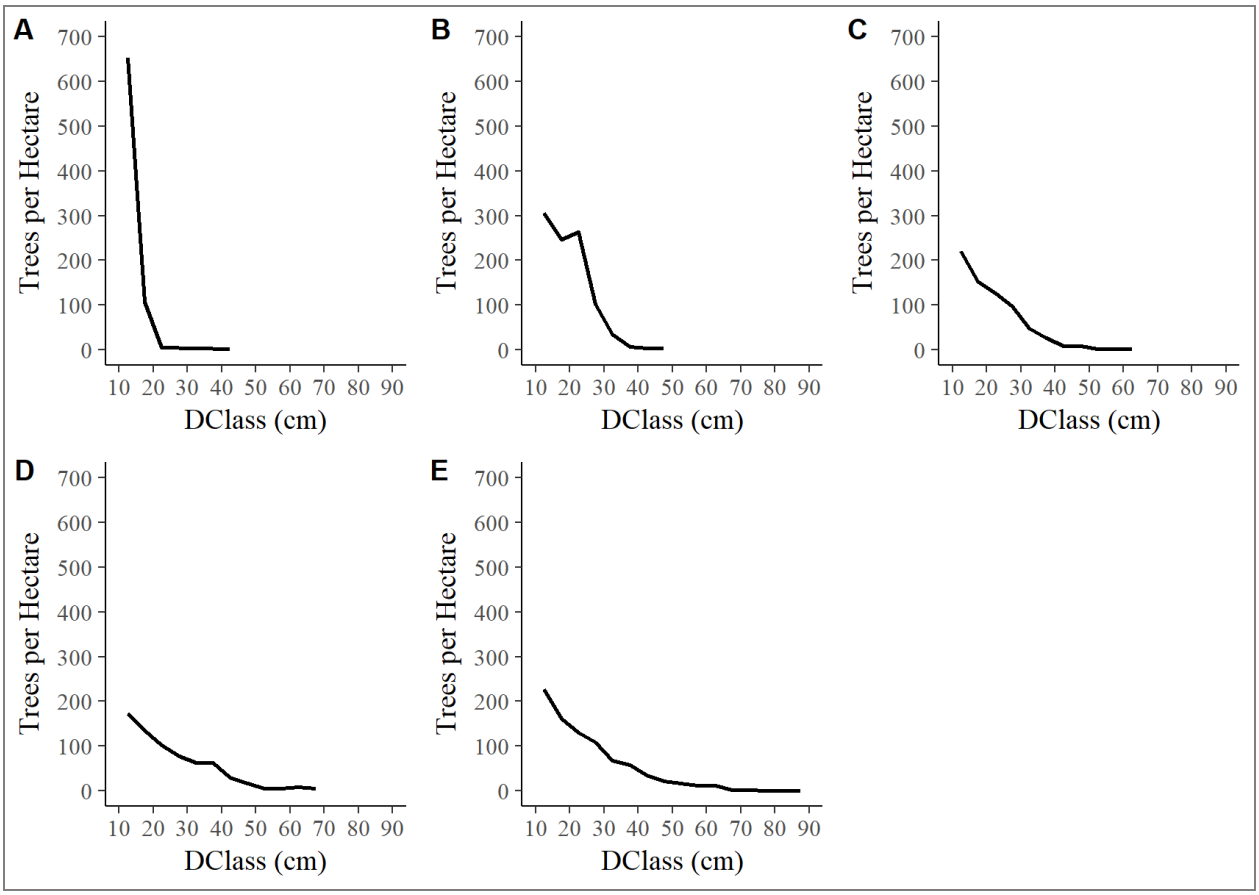

Figure 4-4. Live-tree size distribution for the A) 1990s cohort, B) 1960s , C) 1950s, D) 1930s , and E) matrix cohorts.

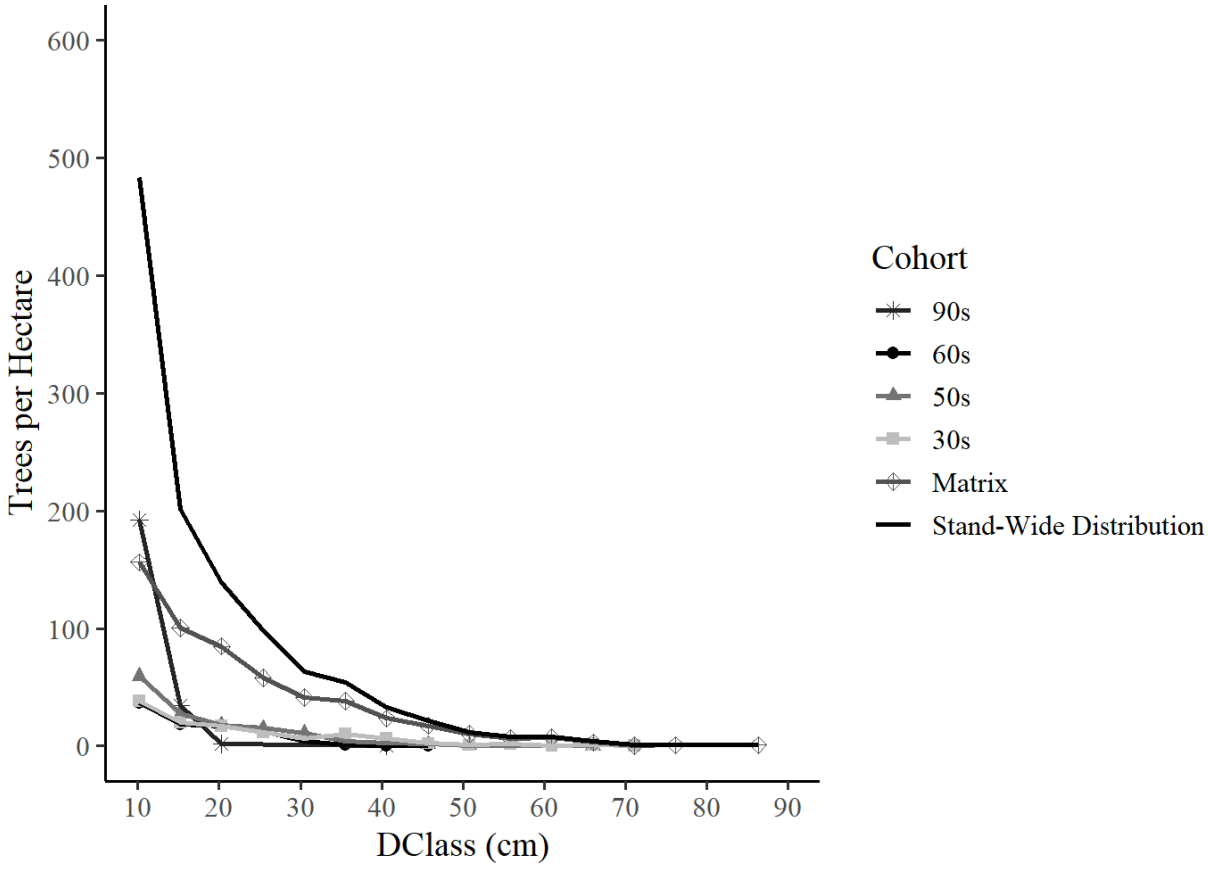

Figure 4-5. Average stand-level, live-tree size distribution weighted by cohort area.

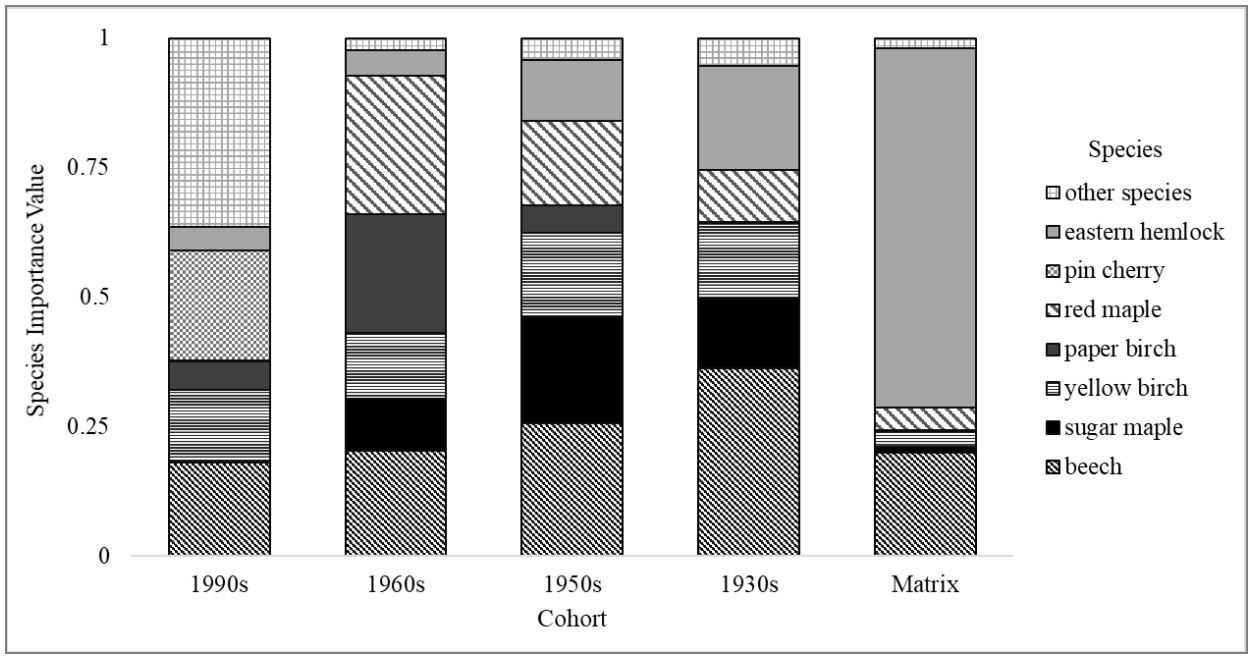

Figure 4-6. Species importance value by cohort.

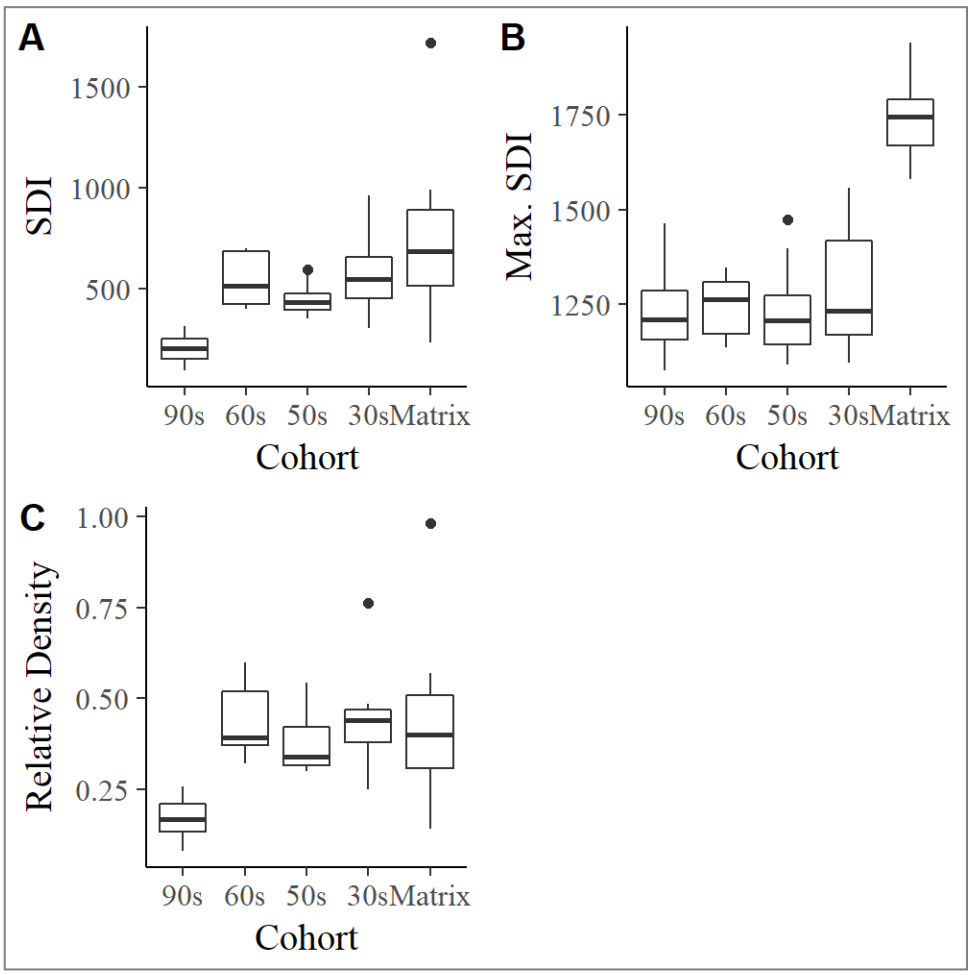

Figure 4-7. (a) Stand density index (SDI), (b) maximum SDI, (c) and relative density by cohort of overstory trees.

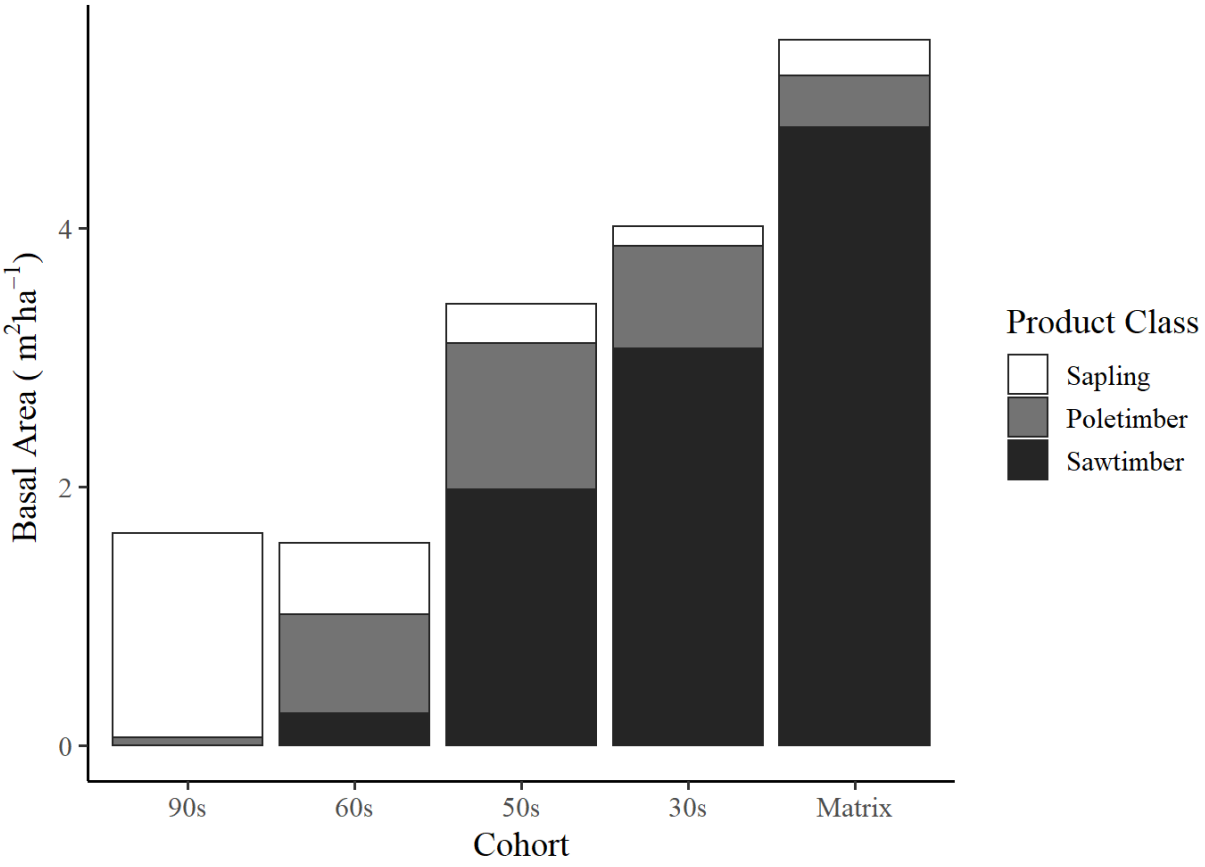

Figure 4-8. Basal area of standing dead trees by product class and cohort. Stand-wide basal area of snags was 3.6±0.5 m2ha-1.

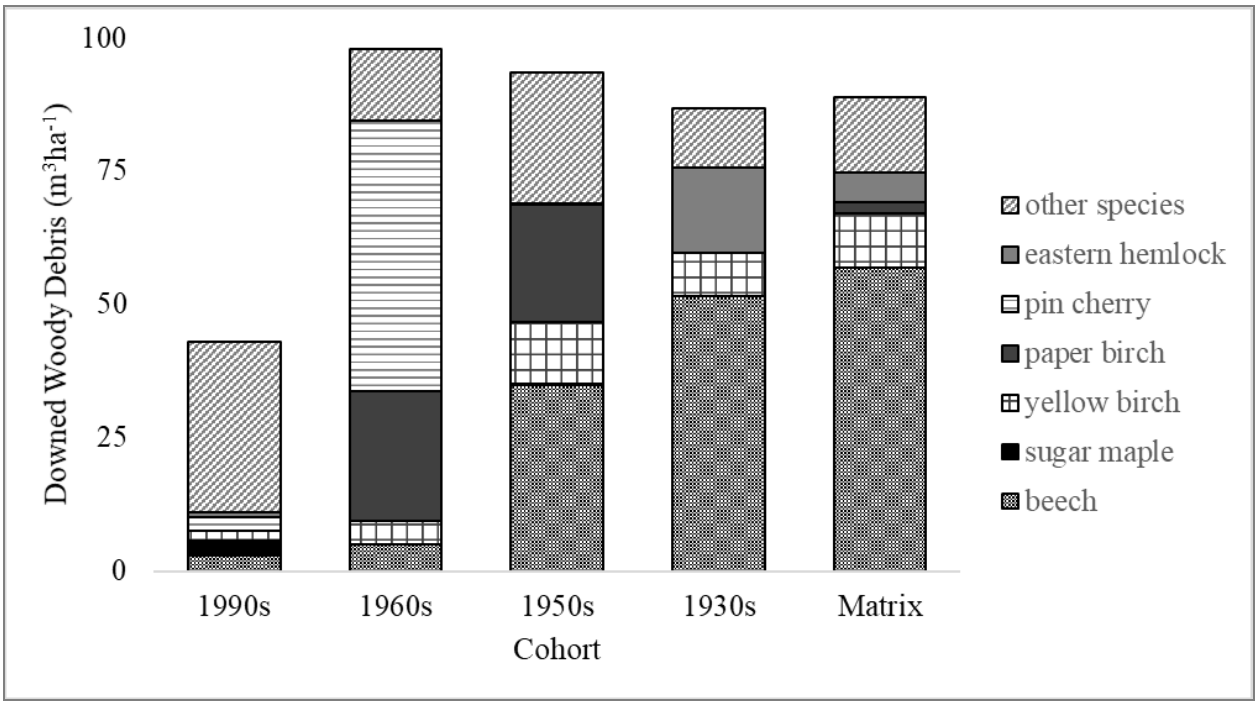

Figure 4-9. Downed woody material volume by species and cohort. Stand-wide volume of downed woody material was 73.5 ±9.8 m3ha-1

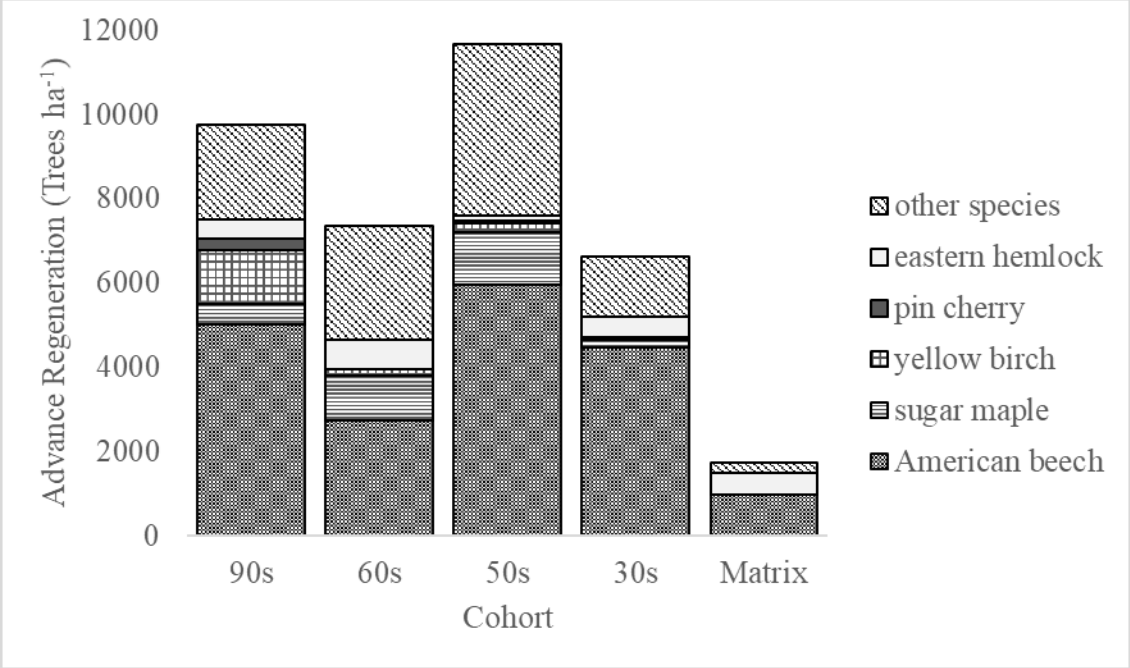

Figure 4-10. Density of advance regeneration by species and cohort.

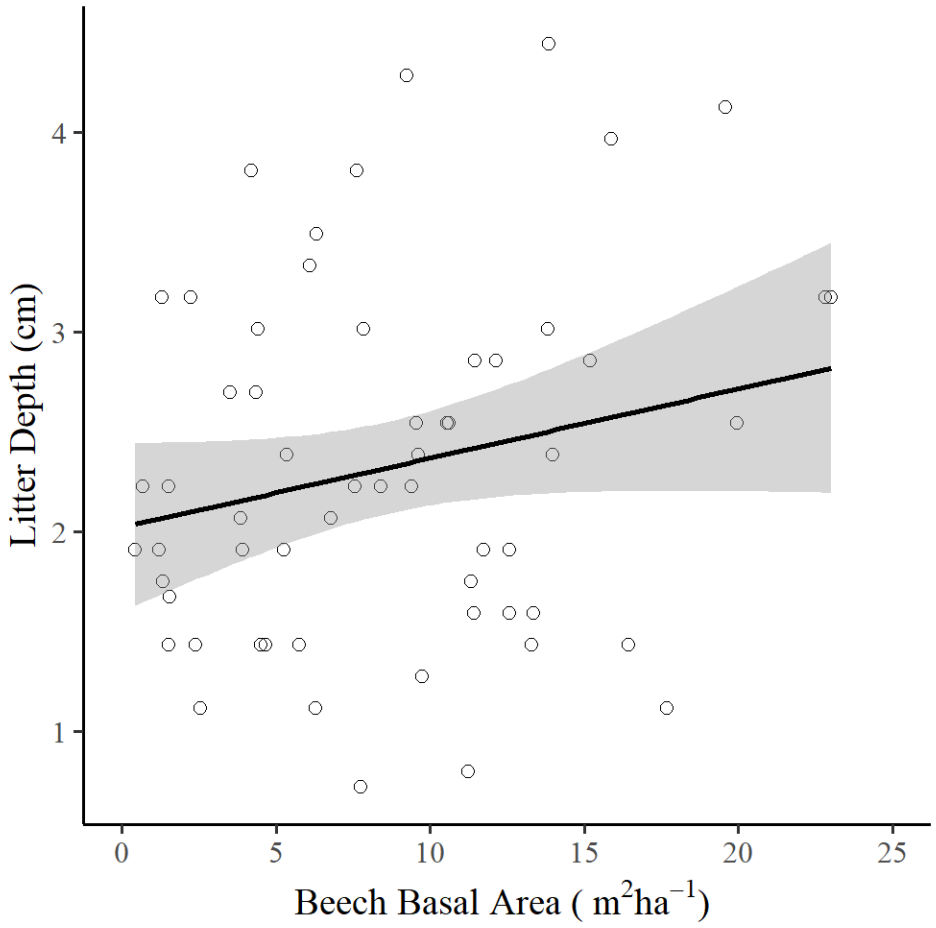

Figure 4-11. Litter depth by beech basal area with simple linear regression trend line and 95% confidence interval.

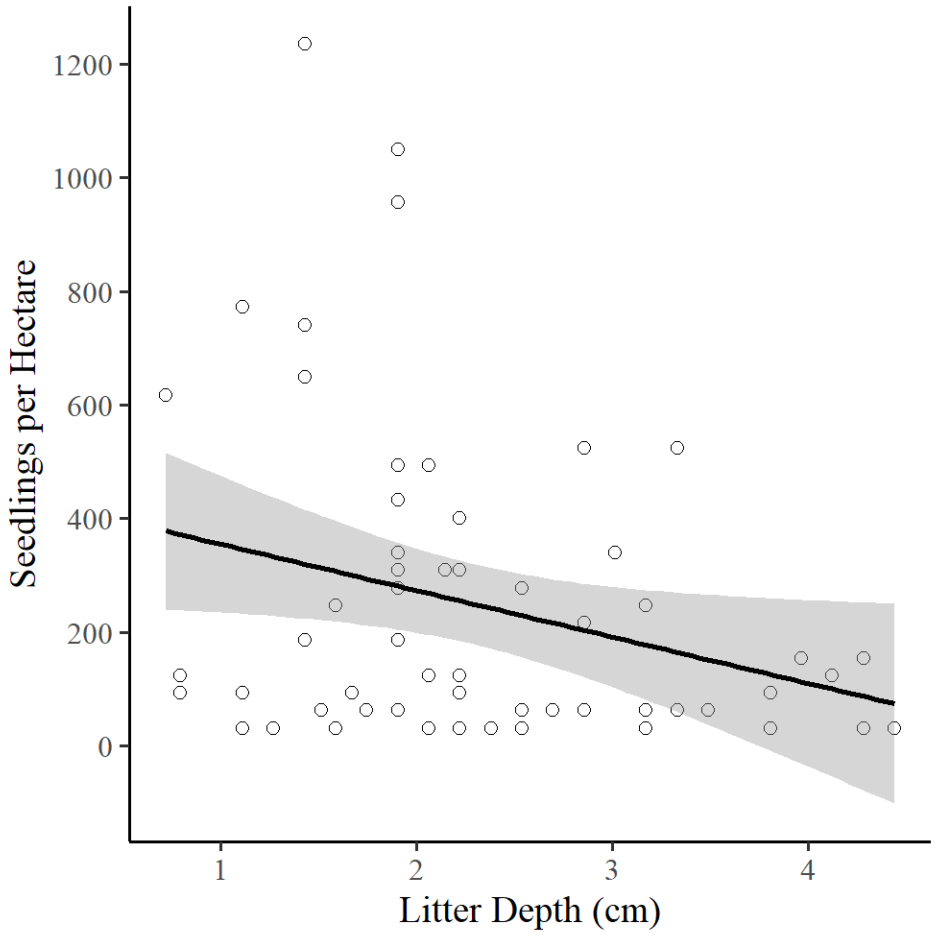

Figure 4-12. Seedling density of sugar maple and yellow birch by litter depth with simple linear regression trend line and 95% confidence interval.

Tables

Table 4-1. Attributes for managed and matrix cohorts.

Cohort	Average Area (Hectares)	Min. Area (Hectares)	Max. Area (Hectares)	Total Area (Hectares)	Plot Count
1 (1937-1940)	0.1	0.0	0.3	3.4	28
2 (1951)	0.2	0.1	0.3	6.4	36
3 (1960)	0.3	0.1	0.8	3.2	11
4 (1992-1994)	0.3	0.1	0.9	5.8	19
5 (Matrix)	NA	NA	NA	26.4	NA
Managed Cohort	0.2	0.0	0.9	18.8	94

Table 4-2. Stand-level species importance values

Species Group	Importance Value
American beech	0.23
sugar maple	0.07
yellow birch	0.09
paper birch	0.04
red maple	0.09
pin cherry	0.02
eastern hemlock	0.39
other species	0.07

Table 4-3. Stand regeneration stocking and density by species group

	Species			
	American beech	sugar maple	yellow birch	other species
% Stocking	93.6	51.0	36.2	54.9
Advance Regeneration Density (tree ha^{-1})	9,450	1,499	817	5,290
Seedling Density (tree ha^{-1})	17,875	4,791	7,592	15,484

Table 4-4. Shannon's diversity index (H) for diameter class by cohort

Cohort	H Diameter
1990s	1.04
1960s	2.14
1950s	2.4
1930s	2.68
Matrix	2.74

Appendix

Appendix A. Number of Sample Plots by Cohort

Cohort	Total Area (Hectares)	# of Plots
1 (1937-1941)	3.4	9
2 (1951)	6.4	16
3 (1960)	3.2	8
4 (1992-1994)	5.8	15
5 (Matrix)	26.4	33
	Total	81

Appendix B. Calculated variables representing forest structure, composition, mortality, and regeneration dynamics.

Characteristics	Variable
Structure	Stand Density Index (SDI) Average Growth Rate Basal area Shannon's Diversity Diameter Class (HDiam) Course Woody Material Standing Dead by Product Class
Composition	Species Importance Value (IV)
Mortality	Average mortality rate by density
Regeneration Dynamics	Density Advance Regeneration Stocking Advance Regeneration Litter depth

Appendix C. Polynomial model summary used to determine diameter distribution shape

	Estimate	Std. Error	T Value	P Value
Intercept	+540.61	38.86	38.86	< 0.05
DBH	-91.63	10.17	10.17	< 0.05
DBH^2	+4.88	0.72	0.72	< 0.05
DBH^3	-0.08	0.14	0.01	< 0.05

Table D. Average litter depth (cm) and standard deviation by cohort

Cohort	Litter Depth (cm)	Std. Dev.
90s	2.25	0.90
60s	2.36	1.11
50s	1.83	0.47
30s	1.76	0.69
Matrix	2.86	0.80

CONCLUSIONS

Identifying the silviculture and management regimes best suited for sustaining northern hardwood forests has been the work of countless scientists and practitioners over the past century. Observations from across the northern hardwood ecosystem and this body of research have demonstrated that a universal approach is difficult to come by with silvicultural options varying by forest ecological conditions, objectives, and past management. Collectively, this underscores a great deal of flexibility in approaching the management of this resource, which may become increasingly important as challenges such as climate change and invasive species increasingly manifest in the future.

The goal of this research was to synthesize the response of northern hardwood forests in the Northeast to a suite of silvicultural systems, site conditions, timeframes, and scales of management. We sought to measure this response through shifts in species composition, stand structure, and regeneration. We also aimed to evaluate the current northern hardwood resource, identifying drivers of forest developmental success and limiting factors. The objectives of this work were explored through four distinct, but complimentary chapters, key findings from each are outlined below.

Main Outcomes and Management Implications

Chapter 1: *Northern Hardwood Silviculture at a Crossroads: Sustaining a Valuable Resources under Future Change* found evidence and support for use of many silvicultural systems, ranging from clearcuts to single-tree selection, across hardwood forests in the northeast. The many unique and challenging conditions faced by forest managers were also revealed, including detrimental impacts of browsing, shifting

composition with increasing American beech, differences in treatment outcomes by site, silvicultural options with changing climate. Application of broad regional prescriptions without consideration of these conditions led to inconsistent results in forest composition, structure, and regeneration establishment. Moreover, the advent of contemporary objectives related to biodiversity conservation and adaptation has increased the need for silvicultural systems flexible to uncertain future conditions. Analysis of FIA data in Chapter 1 stressed the variability in of hardwood forests in the Northeast. This analysis also showed emerging differences between overstory and regeneration composition, especially with regard to American beech. Total regeneration across the northeast remains abundant, but maintaining diversity and composition of commercially and ecologically valuable species is difficult. Future silvicultural systems in these forests will need careful consideration of site quality and influential attributes to ensure a healthy northern hardwood ecosystem.

Chapter 2*: Identifying Factors Affecting Regional Patterns of Sugar Maple Regeneration in Northern New England and New York* took a more detailed examination of the regeneration findings from Chapter 1. Again using FIA data, specific analysis of regional factors affecting sugar maple regeneration revealed the challenges to maintaining this species. Results emphasized the importance of physical site characteristics, including latitude, longitude, and elevation, for sugar maple success. Silvicultural systems aiming to regenerate sugar maple should incorporate these site conditions accordingly. Chapter 2 also found American beech in the overstory and regeneration layers to be a deterrent to sugar maple establishment and growth, again

underscoring the need for beech control in northern hardwood forests if management goals include maintaining sugar maple as a canopy tree species.

Chapter 3: *Long-Term Regeneration Dynamics across a Range of Silvicultural Intensities and Sites in Northern Hardwoods* focused in on site-level outcomes of northern hardwood silviculture using a collection of long-term studies in New York and New Hampshire. Changes over time following commonly applied silvicultural systems revealed the strong connection between site attributes, names soil properties, and baseline species composition. Chapter 3 also highlighted the difficulty of minimizing American beech dominance on poor to moderate sites without direct beech control. In absence of herbicide application or other beech management, silvicultural systems with greater canopy disturbance provided the best option for maintaining sugar maple and yellow birch across sites.

Chapter 4: *Long-Term Evolution of Composition and Structure after Repeated Group Selection over Eight Decades* utilized inventory measurements from the oldest, continuously maintained, group selection study in North America and tracked development of individual cohorts over time. Results showed cohorts in group selection treatments incorporate beneficial attributes of even-age forests, such as composition of mid and intolerant species, while retaining uneven-age structural characteristics at the stand level. This outcome has important implications for management of northern hardwood forests on lower quality sites where species and structural diversity are primary objectives. Chapter 4 also evaluated the influence of beech litter on establishment of sugar maple and yellow birch seedlings, with findings lending support to previous studies

that have postulated a negative relationship between beech litter depth and decline of desired regeneration.

Cumulative outcomes from this work reveal the regionally persistent problem of American beech in northern hardwood forests. Although this species was historically an important component of northern hardwood forests, contemporary stressors, including beech bark disease, elevated herbivory, and changes in soil nutrient status due to atmospheric deposition, have generated novel beech dynamics that greatly complicate the ability of managers to meet compositional and structural targets historically guiding many silvicultural systems. However, results from all chapters suggest best options moving forward require careful review of site level attributes and full consideration of all available silvicultural tools. Maintaining a healthy and diverse northern hardwood ecosystem is essential for meeting existing management objectives and withstanding inevitable future change.

Future Directions

This dissertation provides crucial knowledge for the management of northern hardwood forests of the Northeast United States, but also established a baseline for additional research into this important ecosystem. Under the constraints of time and available data, we focused many results on northern New England and New York, but the northern hardwoods cover a much broader space, including more enriched sites than were evaluated. More analysis of silvicultural outcomes across site conditions and geographic ranges would immensely add to our understanding of how this forest type responds to management and changing surroundings. Silvicultural systems included in this work were also more traditional in nature, inclusion of evolving methods like irregular shelterwoods

or systems designed to mimic specific disturbance regimes may have led to different conclusions. Importantly, this work also advocates for the value and necessity of long-term silvicultural studies. Our findings and research would not be possible without the insights learned from decades of measurements and documentation.

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